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WHAT IS NATURAL? PHILOSOPHICAL ANALYSIS AND YELLOWSTONE PRACTICE

Paul Schullery[1]

EDITOR'S NOTE.—The following remarks were Paul Schullery's introduction to a roundtable discussion presented during the 5th Biennial Scientific Conference on the Greater Yellowstone Ecosystem, held 11–13 October 1999 in Yellowstone National Park. His remarks serve a second purpose in this issue of the WESTERN NORTH AMERICAN NATURALIST, as they set the stage for and introduce the remaining articles, all of which are papers, presentations, or addresses from that conference. The 1999 Yellowstone Biennial Conference was entitled "Exotic Organisms in Greater Yellowstone: Native Biodiversity Under Siege." Mr. Schullery is a resource naturalist with the National Park Service in Yellowstone.

It is probably true that most of us, if we think at all about the people who established Yellowstone National Park in 1872, tend to see them as being essentially like us, only rather stupid. We see them primarily as being at the opposite end of Yellowstone history, totally deprived of all the things we have learned in the past 127 years.

This attitude toward our ancestors probably guarantees that 100 years from now our descendants will be justified in thinking the same about us. Yellowstone's founders were not just dumbed-down versions of us. They inhabited a remarkably different world and responded to cultural and natural environments we seem hardly to understand today. A few examples should make the point.

First, in 1872 the Industrial Revolution was accomplishing the urbanization and mechanization of society. Both changes swiftly divorced people from daily contact with nature. Think of it—after thousands of years, suddenly large numbers of people no longer depended, on a daily basis, on animal power. They no longer saw and handled animals as part of life's most local routines. They no longer expected or required any kind of behavior from nonhuman beings with whom they had grown up.

Historians have traced the increasing popularity of a long-existing humane movement to these momentous changes. People now had the luxury of caring about the treatment and well-being of animals, in part because they no longer had to count on those animals for society's most miserable chores.

Second, in 1872 there were very few adult American memories that were not struggling with or fleeing from personal horrors of the Civil War. This was a societal trauma unlike anything the nation had experienced before, or would experience later. Those of us living today probably cannot comprehend the magnitude of the nation's post-traumatic stress in that first post-war generation.

Third, in 1872 these same people were caught in the first shock waves of the Darwinian revolution. *The Origin of Species* was published in 1859, and *The Descent of Man* appeared the year before Yellowstone was created.

In this unprecedented intellectual, emotional, and cultural turmoil, it is hard to imagine a generation in greater need of Yellowstone, except perhaps our own. But each generation has its own set of needs, and Yellowstone has been responsive to all of them. Perhaps the most important and least understood among those needs are those related to human values. We tend to think of national parks as being good for things we can define, such as recreation and commerce. We are much less comfortable, especially those managers among us, considering the spiritual and emotional aspects of Yellowstone; successful management of public lands is generally defined as numbers: recreational visits per year, regional income generated by tourist dollars, board feet of lumber, tons of ore extracted. This is unfortunate, for although it is true that Yellowstone undeniably has been one of the world's

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foremost "natural laboratories" (to use an early phrase applied to the park) and that it indeed has been a similarly important laboratory of ideas, it is also true that human values underlie all other roles Yellowstone plays in our culture.

Consider those people who established Yellowstone National Park in 1872. Whatever their knowledge and ignorance of geology or ecology, think of their values and then of ours. They killed predators on sight and poisoned carcasses of ungulates in hopes of additional random killing. Without much thought or premeditation, they disenfranchised the native humans of the Yellowstone region. They desperately wanted to improve the Yellowstone landscape in countless ways most modern Yellowstone enthusiasts do not even know were discussed: an elevator to the foot of the Lower Falls of the Yellowstone River; railroad tracks to the geyser basins and beyond; roads through the Thorofare, over Bighorn Pass, around Yellowstone Lake; a system of dams in the Bechler country. They piped water from hot springs for commercial bathhouses; they trashed scores of aquatic ecosystems that had taken thousands of years to evolve; they turned wild bears into garbage dump clowns. In these and many other ways, they changed the place. They did not do these things because they were stupid (though some of them certainly were, just as some of us are). They did them because their view of nature, and of their relationship with it, was substantially different from our own. Most of them did not see these things as wrong; most of us do. They did not have our values, but that does not mean they were without values.

Yellowstone has weathered our stumbling efforts to apply human values to wilderness settings in surprisingly good shape, but it would be foolish to think that we, at the beginning of the 21st century, have arrived at some finished form of the national park. National parks are institutions that must always adjust. The test of an institution's success over the long haul is how responsive it remains to the changing needs of the society that created it. The test of a society over the long haul is its ability to change its institutions only enough to keep them true to whatever high impulses led to their creation in the first place. Yellowstone tests us just as rigorously as we test it.

This conference on the Greater Yellowstone Ecosystem gives us an opportunity to consider where we are today in this very complicated and often painful process of revising our understanding of national parks. Nonnative species provide us with a host of stimulating case studies that do more than perplex policy makers and managers. They reach deeply into our belief systems; they expose the rawest emotional underpinnings of the institution to the often unkind light of day. Best of all, they make us think.

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DEFINING AND EVALUATING EXOTIC SPECIES: ISSUES FOR YELLOWSTONE PARK POLICY

Ned Hettinger[1]

ABSTRACT.—Exotics are species that are foreign to an ecological assemblage in the sense that they have not significantly adapted to resident biota or to local abiotic conditions, and resident species have not significantly adapted to them. Although they need not be human introduced nor damaging, when they are, a negative appraisal of such exotic species can be justified. Human introduction of exotics into natural systems typically increases human influence over those systems, thus diminishing their wildness. Valuing nature for its wildness is a rationale for the national parks' policy of letting nature take its course. Thus, Yellowstone Park has a strong reason for removing human-introduced exotics and for welcoming naturally migrating exotics. Disvaluing exotics that are neither human introduced nor damaging simply because they are foreign smacks of xenophobia. But given that wanton human mixing of species threatens to homogenize the earth's biological communities, biological nativism is justified as a way to preserve the diversity between such communities.

Key words: exotics, exotic species, native, nativism, Yellowstone, wild, natural, biodiversity.

There is considerable debate about how we should characterize exotic species (Scherer 1994, Woods and Moriarty 2001). Controversy concerning the negative evaluation of exotics is also significant (Pollan 1994, Throop 2000). In Yellowstone National Park these conceptual and valuational issues make a difference for policy and management. This paper provides suggestions for how we should define and evaluate exotic species, with particular reference to exotics in the greater Yellowstone region.

DEFINING EXOTICS

Exotic species are defined in many different—even contradictory—ways. The definition I propose aims to separate the distinct strands typically woven into this concept while still capturing most of our fundamental intuitions about exotics. I suggest that we define an exotic species as one that is foreign to an ecological assemblage. In contrast to a native species, an exotic species is one that has not significantly adapted to resident biota or to local abiotic conditions, and—perhaps more importantly—resident species have not significantly adapted to it. When an exotic first arrives, it will not yet have exerted selective pressure on local species, nor will it have responded to selective pressure from the resident species or local abiotic conditions. Once this process of "evolutionary accommodation between newcomer and residents" (Westman 1990) has begun, the exotic species starts the process of naturalizing. At some point the mutual adaptation between immigrant and natives will be significant enough for the one-time exotic to have naturalized and become native (Hettinger 2001).

For example, the protozoan parasite (*Myxobolus cerebralis*) that causes whirling disease (an affliction that cripples some fish species) is a recent immigrant to Yellowstone's ecosystems. A European import arriving in this country about 45 years ago and first detected in park waters in 1998, the whirling disease parasite is exotic to the extent that it has not significantly adapted to species present in the park and to the extent that park natives have not significantly adapted to it. Although the microbe has successfully parasitized some Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*), there has been little time for cutthroat trout to adapt to the parasite or to exert selective pressure on it.

Whether a species is exotic to an assemblage is a matter of degree. The greater the differences between the species, the abiota, and their interrelationships in the old and new habitats, the more exotic the immigrant will be.

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For example, mountain goats (*Oreamnos americanus*) that are moving into the park from the north are likely to be much less exotic to the Yellowstone assemblages they join than Japanese snow monkeys (*Macaca fuscata*) would be in the thermal areas of the park. Mountain goats have likely adapted with a number of species in the park, whereas little if anything in the park has ever adapted with any species of monkey.

Exotic arrival should be distinguished from range expansion where the traveling species does not move into ecological assemblages to which it has not already adapted. Thus, as bison (*Bison bison*) expand their range north and west out of Yellowstone Park into the surrounding grasslands, they enter a habitat in which they are native, because these assemblages and bison have significantly adapted to each other. When the U.S. Fish and Wildlife Service moved gray wolves (*Canis lupus*) from Canada into the park, this was not exotic introduction because gray wolves have evolved with elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and moose (*Alces alces*), among other species present in the park.

Contrary to a frequently adopted definition, including one used by the National Park Service (National Park Service undated), exotics need not be human-introduced species. This is true both because some human-introduced species are native (e.g., the restored Yellowstone wolves) and because some species move to foreign ecological assemblages on their own. Examples of the latter include Cattle Egrets (*Bubulcus ibis*) blown from Africa to South America and the first finches on the Galapagos Islands.

Exotics also should not be identified with damaging species, as some suggest (Scherer 1994), for some natives are damaging and some exotics are not. For example, the Asian long-horned beetle (*Anoplophora glabripennis*), recently discovered in trees in Chicago, is an important threat to trees in its native range as well (Corn et al. 1999). The National Park Service has management policies to deal with such native pests (National Park Service 1988).

It is true that exotics have caused massive amounts of damage, both ecologically and economically (Office of Technology Assessment 1993). Approximately 40% of threatened or endangered species on the U.S. Endangered Species lists are at risk primarily because of exotic species (Pimentel et al. 1999). Nevertheless, exotics need not be harmful. Many, perhaps most, immigrant species in foreign assemblages die out before they become established (Westman 1990, Williamson and Fitter 1996). One estimate is that about 10% of such immigrants succeed in establishing themselves (Bright 1998). Even those that become established need not be invasive or weedy (Mack 1996). Approximately 15% of foreign species that have established themselves in the U.S. have become serious problems (Simberloff 1997). The National Park Service's division of exotics into innocuous species and disruptive species reinforces the point that exotics need not be harmful (National Park Service undated). Making such a distinction is not without risk, for exotics that establish themselves in benign ways may eventually experience explosive growth that damages local assemblages (Simberloff 1997). Still, some exotic species are benign and some are even beneficial. Invasion biologists talk about the crucial role invaders have played in stimulating evolution (Vermeij 1996). In Yellowstone Park, grizzly bears (*Ursus arctos*) and other wildlife consume substantial amounts of nonnative clover (*Trifolium* spp.; Reinhart et al. 1999). A species of eucalyptus tree introduced into California from Australia over 120 years ago benefits monarch butterflies (*Danaus plexippus*) that rely on them during annual migrations (Woods and Moriarty 2001). Eucalyptus also benefits native birds and salamanders (Westman 1990). The common apple tree (*Malus sylvestris*) is an import from Europe and west Asia. It is hard to imagine that this tree has not benefited the North American landscape.

EVALUATING EXOTICS

Justifying a Negative Appraisal of Exotics

Although I do not think we should define exotic species in these ways, the exotic species typically of concern to the park (and others) are both human introduced and damaging. Each of these features provides a strong reason for a negative evaluation of such exotics and perhaps for a policy of control or eradication of them.

A negative evaluation is fairly straightforward when exotics significantly damage human interests or when they impoverish ecosystems, for example, by turning diverse native communities into single-species areas unable to support other life forms. I say fairly straightforward because human interests are not the only ones at stake and because criteria are needed to distinguish changing ecosystems from damaging them (Throop 2000).

A negative evaluation is also called for when an exotic is human introduced. Although controversial, such a value judgment is justified by the following considerations: (1) the fact of ongoing massive human influence on the planet (Vitousek 1997) and the radical diminishment of the sphere of wild nature; (2) a positive evaluation of natural systems to the extent that they have not been influenced by humans, that is, to the extent that they are wild (Hettinger and Throop 1999); and (3) a judgment that the presence of human-introduced aliens lessens the wildness of natural systems and thus provides a reason for disvaluing such exotics.

For example, Yellowstone Lake has been humanized by the introduction of lake trout (*Salvelinus namaycush*), and the park is less wild as a result. Even though lake trout have been present in other park lakes for about a century (Schullery and Varley 1999), their recent introduction into Yellowstone Lake significantly increases human influence over park processes as their presence in that lake threatens Yellowstone cutthroat trout and other species that feed on cutthroat trout, including grizzly bears and Bald Eagles (*Haliaeetus leucocephalus*). Rather than feeling in touch with wild natural processes, a knowledgeable angler who catches a 10-pound lake trout while fishing for cutthroat trout in Yellowstone Lake will be reminded of humans and their ill-advised acts. Removing these lake trout will make Yellowstone a wilder, less human-influenced place, as did closing the garbage dumps to grizzly bears.

Letting Nature Take Its Course

Valuing nature for its wildness is a rationale for the park's policy of letting nature take its course. One implication of seeing the park as a natural area where human influences should be minimized is that just as the park has a reason to eradicate or control human-introduced exotics, so too it has a reason to welcome naturally dispersing aliens. Removing such exotics would seem to increase, not decrease, the human control and manipulation of natural systems in the park.

Those who believe that the purpose of national parks is to "preserve vignettes of primitive America" (Leopold et al. 1963) may argue that the park should eradicate even naturally arriving exotics, for they will alter the character of the native ecosystems the park should preserve. But national parks ought not to be in the business of trying to prevent nature from changing on its own. Yellowstone Park should preserve natural processes, not some particular status quo in nature. The national parks' management guidelines count naturally arriving exotics as "natives" and thus presumably sanction their arrival (National Park Service undated).

Although Yellowstone Park has a strong reason to welcome naturally dispersing exotics, the policy of letting nature take its course is not absolute. Such a policy could be overridden if an exotic—or native, for that matter—were to cause sufficient damage. If the whirling disease parasite somehow traveled from Europe into Yellowstone Park without the aid of humans, the park would be hard pressed to justify welcoming such a naturally dispersing exotic. If the parasite threatened to destroy the entire Yellowstone cutthroat population, the park would have strong reasons not to let nature take its course.

Disvaluing Exotics As Such

Are there reasons for disvaluing exotics per se, simply because they are foreign? If so, the park would have a reason not to welcome naturally dispersing exotics, even when they did not cause damage. But negatively evaluating a species simply because it is foreign smacks of xenophobia and a nativist desire to keep locals pure from "foreign biological pollution." In human affairs, such an attitude is morally repugnant. Nativist fear of foreigners and prejudice against immigrant peoples are morally troubling attitudes. Critics of biological nativism (i.e., the preference for native flora and fauna) point out that the Nazis had a native plant movement and attempted to purify the flora and fauna of their country as they purified their culture of Jews (Pollan 1994). One writer warns that "nativist trends in Conservation Biology have made environmentalists biased against alien species" and thinks it important to "protect modern environmentalists from reproducing the xenophobic and racist attitudes that have plagued nativist biology in the past" (Peretti 1998).

But biological nativists do not dislike foreign flora and fauna, and the charge of purism ignores their commitment to biodiversity. Biological nativists want to preserve the spectacular diversity between biotic communities. The wanton human mixing of species from around the globe creates mongrel ecologies and threatens to homogenize the earth's biotic communities (Hettinger 2001). The logical end point of the massive, human-induced spread of exotics is that ecological assemblages in similar climatic and abiotic regions around the world will be composed of the same species. This biotic impoverishment is much like the impoverishment of cultural diversity resulting from economic globalization and the cosmopolitanization of humans. Keeping a dandelion (*Taraxacum officinale*) out of Yellowstone is much like keeping Wal-Mart out of a small New England town or McDonalds out of India. Kudzu (*Pueraria lobata*) in the American South is like TV in Nepal, a threat to the diversity of the planet's communities and ways of life. Because humans have introduced so many alien species into so many of the earth's biotic communities, the park may well have a reason to oppose even naturally dispersing and nondamage-causing exotics.

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THE NATURALNESS OF BIOLOGICAL INVASIONS

Daniel B. Botkin[1]

Key words: balance of nature, ecosystem dynamics, natural invasions, exotic species, invasive species, National Park Service policies.

The National Park Service has precise policies regarding biological invasions. These place specific burdens on park management. In considering how to handle biological invasions in the United States national parks, we need to be cognizant and sensitive to these requirements. The problems posed by these policies are revealed by an interesting conundrum about invasive species.

CONUNDRUM

A serious conundrum exists about invasive species: Biological invasions are natural and necessary for the persistence of life on Earth, but some of the worse threats to biological diversity are from biological invasions. It was once believed, both among scientists and in prescientific history in Western thought, that nature undisturbed was in a steady state. If this were true, then biological invasions would be unnatural, and management of biological invasions would be simple: prevent them or, if that failed, eliminate the invaders and restore the "natural" steady state. But findings in environmental sciences in the latter part of the 20th century confirm that natural ecological systems are always changing, that they do not have a single steady state, and that biological invasions are natural and, more important, necessary for the persistence of life. If species never invaded new territories, they would be extinguished by catastrophic events in their previous habitats. An additional conundrum is revealed. One can either preserve a "natural" condition, or one can preserve natural processes, but not both. The preservation of natural processes requires change. The resolution to this second conundrum is, however, simple: either preserve the natural processes and therefore preserve life over the long run, or preserve a single condition and either threaten the persistence of life or else substitute a great amount of human intervention for natural, dynamic processes.

Salmon exemplify the necessity of change and of biological invasiveness. Contrary to the folktale that salmon always return to spawn in their natal stream, approximately 15% of adult salmon find their way to a different stream from the one in which they were born (Botkin et al. 1995). This might seem to be a "mistake," but without such "mistakes" salmon could not persist. Salmon are cold-water fish and make use of cold rivers and streams near northern continental glaciers. As glacial ages wax and wane, streams once suitable to salmon become iced over, while others, previously too warm, become sufficiently cold to support salmon. Other natural disturbances make individual streams temporarily unusable. Salmon require gravel of a specific size range and composition in which to lay their eggs. The source of these gravels is the failure of bedrock headwalls at the upstream end of streams. When such a failure occurs, the gravel dumped into a stream temporarily blocks water flow and makes the stream unusable by salmon. But without such temporary blockages, gravel would slowly erode from all salmon streams. Salmon streams must become temporarily clogged with gravel and therefore temporarily unusable for salmon to survive. Therefore, the requirement for a supply of gravel also requires that salmon be able to shift among streams over time. Fires and storms create conditions that temporarily eliminate salmon from a specific stream, thus also requiring that salmon can move among

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streams. Thus, for salmon to survive over a long time, invasiveness and reinvasiveness are necessary characteristics.

Biological invasion is a natural process everywhere, requisite for the persistence of essentially all species on Earth over the long term. Being able to seek new habitats and survive in them is essential in an environment that changes at all scales of space and time. A striking example occurred with the creation of Surtsey, a new island 25 km off the coast of Iceland as a result of volcanic activity (Botkin and Challinor 1998). In 1964 scientists camping on Iceland's south coast saw the view from the shore dominated by a vertical plume of ejecta and smoke from an open fissure about 100 m below the water surface on the mid-Atlantic ridge. When ocean water met molten lava at that shallow depth, the water pressure was insufficient to contain the resulting explosion, which hurled large pieces of the seabed through the water column as high as 300 meters into the air. Pulsed explosions occurred with each contact of cold seawater and molten lava at the fissure. The rapid cooling of the lava resulted in fine-grained crystal particles called tephra.

About three and one-half years later, in 1967, the explosions ceased, and the volume of tephra that had rained from the sky created Surtsey, roughly two kilometers in diameter and rising at its highest point about 100 meters above sea level. A few weeks after the eruptions ceased, the lava that formed Surtsey had cooled and hardened just enough so that it was safe for a person to walk on the surface, although molten lava was still visible flowing deep below through occasional surface cracks. Now the island could be visited by people. A group of scientists went to the island, and one, a botanist, found the first flowering plant invader: the sea rocket, a small flowering plant less than 5 cm high, and it was already in bloom. That the sea rocket flowered so soon after the lava solidified illustrates the speed with which biological invasions can occur.

Other botanists later discovered mosses and grasses that continued the biological invasion of Surtsey. Scientists formed the Surtsey Research Society, which stimulated long-term monitoring of the invasion process. The invasion of Surtsey by the sea rocket had no negative effects and can only be viewed as a positive event, beginning the transformation of a new but lifeless island into one rich with vegetation and other forms of life.

Another recent, ongoing example of a natural biological invasion that has had little if any negative consequences is that of the Cattle Egret, a ubiquitous white bird familiar to travelers who view African wildlife. This bird probably evolved in the flood plains of the African tropics but adapted to irrigated crop fields, especially in southern Africa. Cattle Egrets eat insects stirred up by or on large grazing mammals. In Africa these birds readily made the transition from following only the wild, native mammalian herbivores to following domestic cattle as the number of buffalo and other large, wild herbivores declined. More surprisingly was the transoceanic migration of this species, which flew from west Africa to South America. Eventually, enough egrets arrived to establish a New World breeding population. In hindsight, this transoceanic invasion was not such a difficult feat for this amazing bird because, if helped by favorable winds, Cattle Egrets can fly the 2900 km from West Africa to South America in about 40 hours.

First reported in South America in the 1880s, the birds rapidly expanded their range, especially as coastal tropical forests were cleared for cattle ranching in the 20th century. Once established in South America, they migrated north, reaching the United States in 1951. Just 5 years later they had spread from Texas to New England—several thousand kilometers!

A similar process took place in Australia, where these birds became common in the western part of the continent in 1952. They reached New Zealand in 1963, and breeding pairs were found about a decade later. The Cattle Egret expanded its range from Africa to virtually all tropical and temperate areas of the Earth within a century. Its expansion was fueled by its ability to exploit pastures with high cattle densities—an artificial habitat more suitable for its feeding behavior than its original one in Africa. So, in part, the egret's migration was assisted by effects of people on nature. But egrets took advantage of these human actions on their own; they were not transported by people. The widespread invasion by egrets seems so far to be benign because it fills a niche heretofore unoccupied by New World birds.

In contrast is a long list of invasions of exotic species that have had disastrous effects. Embarrassing to human judgment, many of the worst cases result from intentional human introduction, fostered with the belief that each would be beneficial. As an example, people in Great Britain intentionally introduced the American grey squirrel into the British Isles, believing this would add aesthetically to their woodlands. But the North American squirrel is forcing out the native British red squirrel, which has been extirpated from much of its original range and persists today only where habitats are inhospitable to the North American squirrel. Another famous example is the gypsy moth, introduced into Massachusetts by a well-meaning scientist who believed these insects could be used to establish a silk industry in North America. He also believed the moth could not spread westward because he introduced it in eastern Massachusetts, and the prevailing westerly winds would keep the moth along the coast.

The history of both positive and negative effects of biological invasions is essential background for the consideration of National Park Service policy regarding biological invasions.

NATIONAL PARK SERVICE POLICIES AND BIOLOGICAL INVASIONS

What are the implications for National Park Service policies toward invasive species, given the conundrum about biological nature—that it is both necessary and natural, and can create major problems in certain situations? According to National Park Service administrative policies, "Non-native species of plants and animals will be eliminated where it is possible to do so by approved methods which will preserve wilderness qualities." This is interesting because (1) the goal is complete elimination, not control, and (2) the definition brings in the term *wilderness quality,* which remains ambiguous and therefore presents operational difficulties.

Furthermore, NPS administrative policies define an exotic species as "a species occurring in a given place as a result of direct or indirect, deliberate, or accidental actions by humans." This definition focuses on the *mode of transportation and arrival* rather than on the *effect* of the species on others and on ecosystems. Further affirming this emphasis on the mode of transportation, National Park Service administrative policies define a native species as "a species that occurs and evolves naturally without human intervention or manipulation." Species that move into an area without the direct or indirect aid of humans are considered native by NPS definition. Based on this definition, a species that arrived without human intervention but completely altered a park's ecosystem from what it was prior to European settlement would be considered acceptable and would be allowed to persist within a park. However, a species that directly or indirectly arrived as a result of human actions, even if its presence was obscure and its effects innocuous, would be a target for elimination. But what if a species that arrives on its own, without human intervention, greatly disrupts the biological diversity of a park and alters its landscapes from the way they appeared just prior to European settlement? And what if a human-introduced species has little effect if any, or increases the bountiful appearance of a park?

This emphasis on the condition of a park prior to European contact appears in NPS administrative policies, which state:

> Plant or animal species introduced by indigenous peoples may be preserved and protected where they were introduced to the site prior to European settlement, and were culturally significant, and where their presence does not have any demonstrated impact of native species.

This means that, by NPS policy, species introduced after 1492 by Europeans are bad and to be exterminated, but those introduced before 1492 by peoples not of European origin are acceptable. In selecting a specific cut-off time for introductions that are to be allowed, there is an arbitrariness in this last policy. Underlying this policy also is the assumption that a single time, which therefore indicates a single state of nature, is the only one that is natural. This policy fails to acknowledge that natural ecological systems always undergo changes, and that a single time period is not an adequate measure of what is "natural."

A goal of returning a park to a specific time is consistent with earlier ideas about nature, in particular with the belief in a balance of nature. This is the idea that nature, left alone, will achieve a single state—a constancy of form and structure that will remain indefinitely (Botkin 1990). As stated earlier, research among environmental sciences in the last 30 years of the 20th century demonstrated this was false, that natural ecological systems are dynamic and changing. The one thing we can be sure about nature in the future is that it will be different from today, because nature is always changing. Therefore, a goal of maintaining a park's ecosystems and species list to conform with what was the condition at a single past time cannot be obtained by a hands-off, do-nothing policy. It requires extraordinary effort. Recently, much lip service has been paid to the idea of the naturalness of change, but policies and actions have lagged behind, most of which are based on some kind of steady-state notion.

The NPS policy is mixed in regard to steady state. It allows natural introductions and introductions by American Indians, but not by those that occurred afterward. The implicit assumption is that introductions following European settlement have had only bad effects while those prior to European settlement had good or neutral effects. This is not true a priori, and it is not necessarily true in fact, as salmon, the sea rocket, and the Cattle Egret demonstrate. As explained earlier, these policies confuse the origin and mode of transport of a species with the effects of that species on the ecological system where it arrives.

Setting Goals

Are we claiming that an invasive species is a problem for the physical system—the ecosystem or a species—that an ecosystem or set of ecosystems cannot persist with *any* invasive species? Or do we desire to eliminate invasive species because of our appreciation of landscape beauty and a belief that the only landscape that can be beautiful in North America is one that was not affected by European civilization? Or do we desire to eliminate invasive species because of a spiritual value, perhaps reasoning that such a landscape might serve as a source of creative inspiration, but again only if it appears as it did prior to any European influence? Do we fear that introduced species, no matter how innocuous or beautiful, will take away from that spiritual or aesthetic quality of an American national park? Or is our justification a moral judgment—that only those species that arrived on their own or were helped by pre-Europeans are morally acceptable?

Let us consider the scientific basis for the argument that all invasive species should be eliminated. While there is ample evidence that many introduced species have led to disasters, I am aware of no evidence to support the generalization that all invasiveness is always negative. The Cattle Egret would appear to provide a sufficient contrary case in terms of ecosystem and landscape dynamics. Therefore, it would seem that a completely general policy opposing invasion of new species since European settlement must be based on nonscientific justifications, such as I have reviewed. These nonscientific reasons are value judgments, which are a personal and societal choice. They can be taken as good or bad, my point being that they cannot be justified on scientific grounds alone.

Discussions of the importance of native species and the negative effects of invasive species typically focus on the scientific basis—on the effects of ecosystem functioning and of the persistence of native species, including the potential extinction of a native species. We tend to shy away from discussing the complex mixture of goals I have mentioned. I think this is in part because of a belief that the intangible values—beauty, spirituality, inspiration, morality—won't sell in our modern, materialistic world. But to the contrary, the history of Western civilization is the history of the great power of ideas and beliefs. Somehow, when it comes to the environment and to life on Earth, we doubt this power.

I submit it is more logical, easier to justify theoretically, and pragmatically simpler to construct policies for invasive species based on truly held values about the intangibles—beauty, spirituality, creativity, morality—than it is to base them on poorly understood and often misused science.

Consider the introduction of wolves into Yellowstone National Park. The introduction of wolves is typically justified on 2 grounds: that they were present in pre-European settlement times, and that they perform a necessary function in the Yellowstone ecosystems, usually stated in terms of the natural control of their prey species. If this is taken to be an introduction, then it might be interpreted as contrary to written national park policy. If it is assumed that the presence of wolves will bring the abundance of its prey species back to the level at some specific year, such as 1492, then modern ecological research has shown that this will not be the case. While large mammalian predators can reduce the abundance of their prey, the idea that they could create a precise control and return a wilderness to a fixed, steady state has been abandoned by the science of ecology. The reintroduction of wolves can be justified on mechanistic grounds (that is, on the basis of their function in Yellowstone ecosystems) only if reduction in abundance, rather than precise control, is acceptable.

These policies and assumptions are not unique to the National Park Service. As I wrote in *Discordant Harmonies,* there are 3 basic kinds of natural areas or nature preserves, when people use that term in North America: (1) an area with no human action, (2) an area set aside to conserve a specific species or species assemblage, (3) an area set aside to represent a particular time, usually taken to be that just before European settlement. In regard to invasive species, NPS policies are consistent with the last of these conceptions of “natural.”

The naturalness of biological invasion gives some substance to the fear of those who live near but outside the park: that a truly successful reintroduction of wolves within the park will lead to their invasion (or reinvasion) of surrounding areas. As long as policies are based on restoring ecological systems to specific prior conditions, but allow little other direct actions, then preventing the spread of wolves beyond the park might not fall under park policies.

Suppose we took a different approach: justifying the introduction (or reintroduction) of wolves into Yellowstone on the grounds that they were once part of the ecological systems, and that people want to see them there, for aesthetic, spiritual, and moral reasons. We abandon the arguments about the ecological role of wolves as a necessary condition for sustaining the Yellowstone ecosystems. If the goal is justified from one of these points of view, then less burden in placed on science. Science does not have to provide the rationale for the presence of wolves. Instead, science can tell us how we can attain the goal of maintaining wolves within the Yellowstone ecosystem with minimal effects outside the park. In this case science plays its natural societal role. Scientific findings tell us what the natural characteristics of Yellowstone ecosystems are, and these include change over time. They tell us what species were present, but provide little information about actual abundances (because of a lack of historical data, both before and after the establishment of modern ecological science). Scientific findings tell us what goals are possible, how we can attain them, and what we gain and give up in achieving a goal.

SUMMARY

A dominant idea in ecology in the 20th century was the belief in a balance of nature—that there is a single true condition for any ecosystem, and therefore a single truth for that system. But modern ecological research shows us that ecological systems can persist under a variety of states and, in fact, generally require some level of variation. Rather than there being a single true condition to which a park must be returned, there are options, which depend on our goals. Allowing the possibility of several options for a park may make some conservationists uncomfortable. It may seem to open up the management of a park to conditions that specific interest groups would find undesirable. What becomes clearer through this discussion is that the management of a national park, rather than simply the restoration of a wilderness by abandonment of human intervention, resembles more the activities of a landscape architect who works to choose a landscape design that meets the real needs of a client. In this case, the client is the citizens of the United States and the visitors to the national parks.

Given the naturalness of biological invasions and the manifold rationales for the conservation of species and restoration of national park ecosystems, I believe that the path I have laid out provides a methodology more consistent with the goals of a democracy, more likely to achieve what people want to see in a park, and more likely to allow flexible management that will maintain biological diversity within a park.

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NATURAL AND UNNATURAL; WILD AND CULTURAL

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ABSTRACT.—Yellowstone National Park's mission and policy can be clarified by analysis of the natural and the unnatural. *Nature* is a comprehensive word, in some uses excluding nothing; more useful is a contrast distinguishing *nature* and *culture.* Specifying "wild nature" denotes spontaneous nature absent human influence. Critics claim that the meaning of wild nature, especially of wilderness, is a foil of culture. Pristine nature, often romanticized, is contrasted with a technological and industrial culture. By this account, wilderness is a social construction.

Nevertheless, wild nature successfully denotes, outside culture, an evolutionary and ecological natural history, which remains present on the Yellowstone landscape, jeopardized by numerous human influences, including the invasions of exotic species. Natural processes have returned in the past, as when Native Americans left the landscape. Natural processes can be preserved today, because of, rather than in spite of, park management. Over much of the North American landscape nature is managed and at an end. Yellowstone provides an opportunity to encounter and to conserve "untrammeled" nature as an end in itself, past, present, and future.

Key words: nature, natural, wild, pristine, wilderness, culture, management, exotics.

1. NATURE AND CULTURE

In one sense, *nature* is quite a grand word, referring to everything. *Natura* or *physis* is the source from which all springs forth. If one is a metaphysical naturalist, then nature is all that there is. The contrast class might be the supernatural, which, they may argue, is an empty set. Humans are generated within nature and they break no natural laws. Everything agricultural, technological, industrial, or economic will, on this meaning, be completely natural. So will everything humans have done, whether intentionally or accidentally, by way of moving animals and plants around, as with exotics and invasive species. So will all park management.

Baird Callicott says, provocatively: "We are therefore a part of nature, not set apart from it. Chicago is no less a phenomenon of nature than is the Great Barrier Reef." Or Yellowstone. Callicott wants to cure us from mistakenly supposing a "sharp dichotomy between man and nature" (1992:16–17). Such scope is problematic, however, because it allows no useful contrast with culture; but we need that contrast carefully analyzed if humans are going to relate their cultures to nature. We need a more restricted definition, one that can enable us to separate Chicago from Yellowstone.

A straightforward contrast is *culture.* If I am hiking across the Lamar Valley, the birds and their nests are natural; but if I come upon an abandoned boot, this is unnatural. Expanding this into a metaphor, the whole of civilization is mind and hand producing artifacts in contrast to the products of wild, spontaneous nature. Wild animals, much less plants, do not form cumulative transmissible cultures, elaborating such artifacts over generations.

Humans evolved out of nature; our biochemistries are natural. We too have genes and inborn traits. But human life is radically different from that in wild nature. Unlike coyotes or bats, humans are not just what they are by nature; we come into the world by nature quite unfinished and become what we become by culture. Humans deliberately rebuild the wild environment. They also deliberately set out to conserve some wild places, as with Yellowstone, protected by an act of Congress.

Information in nature travels intergenerationally on genes; information in culture travels neurally as persons are educated into transmissible cultures. They learn how to build fires, or make spears, or make iron plows and grow wheat. Humans argue about worldviews, about whether there should be wildlands as well as wheatlands in Wyoming. The determinants of

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animal and plant behavior are never anthropological, political, economic, scientific, philosophical, ethical, or religious.

Any transmissible culture, and especially a high-technology culture, needs to be discriminated from nature. Boeing jets fly, as wild geese fly, using the laws of aerodynamics. The flight of wild geese is impressive. The information storage system in goose genetics could, in its own way, be the equal of that by which Boeings fly. Some of the information in the geese is transmitted nongenetically, as when they learn migration routes by following other geese. But geese do not form cumulative transmissible cultures.

It is only philosophical confusion to remark that both geese in flight, landing on Yellowstone Lake, and humans in flight, landing at O'Hare in Chicago, are equally natural, and let it go at that. No interesting philosophical analysis is being done until there is insightful distinction into the differences between the ways humans fly in their engineered, financed jets and the ways geese fly with their genetically constructed, metabolically powered wings. Geese fly naturally; humans fly in artifacts.

2. NATURE AND WILDNESS

Nature goes back to Latin and Greek roots for "giving birth" or "springing forth," roots that survive in *pregnant, genesis,* and *native.* We also have the word *wild,* placed as an adjective to nature. With this significant modifier, some perspectives shift. We wish to make it abundantly clear that we are referring to a world outside the human sector. There is spontaneous nature in humans, as when we digest food. There is human nature, as when parents care for children. In contrast there is wild nature, elemental and spontaneous, with humans out of the picture. The word *wild* is already present in Old Teutonic, the precursor of English, before 450 A.D., and means "not domesticated" or "not cultivated." The word *wilderness* is found in Old and Middle English and means "land not farmed or settled," "land in its natural state" (Chipeniuk 1991).

But, comes a protest, etymologies develop and the meaning of wild is obtained by contrasting it with its foil, culture. Maybe we use a word with a thousand-year history, but we use it in the framework of a modern perspective, one that comes out of Western science and a high-tech culture. This can be seen even more clearly when wild is loaded into our concept of wilderness. Non-Western peoples typically do not have the word *wilderness* in their vocabulary, and even some Western languages (like Spanish) do not have such a word.

Wilderness was once untamed, uncivil nature, nature cursed after the fall of Adam, savage nature beyond the "frontier" which it was the American/European manifest destiny to conquer. Only with the Romantic movement, and still more recently with the modern wilderness movement, did the current concept of wilderness arise, a pristine realm unspoiled by humans. Some of that was initiated in Yellowstone when Americans, busy taming the frontier, paused to wonder whether they might not better save at least this region of wild nature. A century later that ideal continues, as official policy: "The primary purpose of the National Park Service in administering natural areas is to maintain an area's ecosystem in as nearly pristine a condition as possible" (Houston 1971).

But thereby we create a myth, these critics say. Nature-wild is just one way we choose to see nature, especially when we are on vacation in Yellowstone. Wilderness so imagined is a foil for our American culture, a romanticized Garden of Eden. Wilderness enthusiasts have a kind of archetypal, archaic longing for a world with no people in it, imagining it as pristine and pure.

David Lowenthal says: "The wilderness is not, in fact, a type of landscape at all, but a congeries of feelings about man and nature of varying import to different epochs, cultures, and individuals" (1964:36). David Graber explains:

> Wilderness has taken on connotations, and mythology, that specifically reflect latter-twentieth-century values of a distinctive Anglo-American bent. It now functions to provide solitude and counterpoint to technological society in a landscape that is *managed* to reveal as few traces of the passage of other humans as possible. . . . This wilderness is a social construct (1995:124).

Roderick Nash, tracing the history of *Wilderness and the American Mind,* reaches a startling conclusion: "Wilderness does not exist. It never has. It is a feeling about a place. . . .

Wilderness is a state of mind" (1979). "Civilization created wilderness" (1982:xiii). Wilderness is a myth of the urbane, mostly urban, mind. Wilderness is a filter-word with which we color the nature we see. Wild is as much construct as West.

Or so they say. But the trouble is that such critics have so focused on *wild* as a word taken up and glamorized in the term *wilderness,* that they can no longer see that wild and wilderness do have reference outside our culture. It cannot count against wilderness having a successful reference that some earlier peoples did not have the word. Yes, wilderness is, in one sense, a 20th-century construct, as also are Krebs cycle, DNA, photosynthesis, and plate tectonics. None of these terms were in prescientific vocabularies. Nevertheless, these constructs of the mind enable us to detect what is not in the human mind.

Civilization creates wilderness? Lately yes, originally no. More specifically, the U.S. Congress, acting for its citizens, designates wilderness. That is a legislative meaning of create, not the biological meaning. Wilderness created itself, long before civilization; everybody knows that and it is only setting up conundrums to exclaim, "Civilization created wilderness." Wildness a state of mind? Wildness is what there was before there were states of mind.

It ought not to be that difficult for Lowenthal, a geographer, to distinguish between the wilderness idea, which has its vicissitudes in human minds, and wilderness out there, wild nature absent humans. A "congeries of feelings of varying import to various individuals in various epochs" is not any Yellowstone wilderness worth saving. With more denotation with the connotation, there is plenty of surviving objective reference in the word.

We need then to identify what it is in nature to which we so refer. *Wild* gets at those levels in nature where there is mixed stability and spontaneity, creative processes in conflict and resolution. There is a mixture of order and chaos. The reference is not ordinarily to molecular or atomic scales. We do not usually think of a single carbon atom as being wild, nor do we describe crystal structures as being wild. Crystal structures are too orderly. *Wild* retains some of the "uncontrolled" or "unlawful" or "spontaneously autonomous" elements. Originally, the reference is to nature outside human plan and control. But within that domain, the reference continues to nature outside simple lawlike patterns. We do not control these events; neither are they completely controlled naturally. There needs to be more complexity; the complexity needs to have broken symmetries.

Geomorphological and climatological processes qualify better than simple physical and chemical ones. There need not be living things. Antarctica is wild. We probably think of a moonscape as being wild; rocks and debris are scattered there; meteors have left their impact. But eclipses of the moon can be predicted to within microseconds for centuries ahead; the clockwork regularity overwhelms the spontaneity. The process is too automatic to catch what we mean by wild. *Mechanical* is not a synonym for wild. *Wild* needs more evident autopoiesis, more turbulence and ferment.

In biology the negentropic tendencies are there working against the entropic tendencies, generating and testing new possibilities. We are inclined to think genetics more wild than crystallography, although they are equal processes in spontaneous nature. Many processes may be determinate, but there will be the intersection of causally unrelated lines, producing novelty and unpredicted events. Individual events rattle around in the statistics. Recent science accentuates genuine contingency, openness mixed with determinate laws. The result, on landscape scales, is idiographic places, beyond lawlike regularity. Yellowstone is not celebrated as a place where the laws of gravity are obeyed unexceptionally, or because meiosis, mitosis, and photosynthesis take place predictably there, as they do everywhere else. Yellowstone is celebrated because it is like no place else on Earth, no place else in the universe.

3. EXOTICS AND INVASIVES

On such wild landscapes, we also find *exotics,* with the root meaning "from the outside." *Exotic* too is an interesting word, especially because of its alternative meanings. On the one hand, the usual meaning is "intriguing," "charming," "beautiful" because unfamiliar. When one visits botanical gardens, one searches out the exotics. But the Yellowstone meaning is "foreign," "invasive." When one visits Yellowstone, one despises the exotics. Exotics reduce the wildness on the landscape.

But why so? You can still have the unpredictability, the contingency, and the spontaneity when exotics are introduced. Which exotics end up where is as patchy as the mosaics on natural landscapes. Conflict and resolution are still taking place when purple loosestrife invades a pond. If a vacant lot in a city is abandoned, weeds take over. Has not the lot gone wild? Maybe Yellowstone has had some exotics dumped into it; but the new plants are on their own. They do their thing, beyond human control. They might even increase biodiversity, although exotics typically displace native vegetation and are, after habitat destruction, the biggest cause of biodiversity loss in the United States (Enserink 1999).

Yes, but now the wildness is reduced. The temporal continuity with the evolutionary past is broken. The area is less pristine. Perhaps wildness can eventually return. But meanwhile the exotics are making the place unnatural. The invasives are not adapted fits, having evolved on other landscapes and been transported here anomalously. Invasive means "entering by an unlawful force." These plants and animals have not entered these ecosystems by any of the lawlike natural processes that, in the wild, govern community structure. They are, we might say, feral. Feral does not mean "wild."

Exotics do not contribute to what Aldo Leopold called the "integrity, stability, and beauty of the biotic community" (1968:224–225). Charles Elton recognized this, half a century ago: "We are living in a period of the world's history when the mingling of thousands of kinds of organisms from different parts of the world is setting up terrific dislocations in nature" (1958:18). These exotics are, we might say, weeds. But the word *weeds* now has an atypical sense, since these plants are not out of place, undesired, in our cultivated garden. These plants are misplaced in the wild.

Exotics typically grow well in disturbed soil, and humans disturb enormous amounts of soil. So exotics are waifs of culture. One might expect, however, that exotics will fail in wild ecosystems, since they are not good adapted fits. And that is often so. The invasives often linger around culture, on roadsides, in fence rows. One does not find them deep in the wildlands—at least not at first. But there is disturbed soil in nature as well as in culture, and these plants can gradually invade native places, as they have in Yellowstone. Say, if you like, that they did so competitively; it is equally true that they did so by assistance of boat and plow.

We can take *weed* as a metaphor for the whole. One doesn't want a weedy landscape. Initially this means a landscape where fields and pastures are full of weeds that we dislike. Later it means a landscape where wild nature has been invaded with exotics. One doesn't want a garden with weeds. One doesn't want a national park, a natural park, with weeds. On a small scale, relatively, Yellowstone becomes the park of weeds, rather than an evolutionary ecosystem. On a larger scale, Earth becomes a weedy planet, rather than a biosphere.

Yes, comes a reply, but these weeds are invasive and competitive, now on their own, even if once brought to their new locations by human transport. They are like everything else wild, except that they manage to exploit humans and their activities, and to live, wildly, in the nooks and crannies of civilization. When humans set aside wild sanctuaries and parks on the periphery of their civilization, these exotics are poised, ready to test their coping skills in these pockets of wildness in the midst of civilization. Stickseeds evolved to catch on animal fur, but if several seeds catch instead on a hiker's britches and then are dislodged half a mile down the trail, the resulting seedlings do not know whether they were carried by animal or by human; it does not matter. Admire them for their aggressive success; that is what natural selection is all about, ongoing now despite human interference.

It may matter, however, when the britches are carried by jet plane to a different continent, where the sprouting seeds will not have evolved as an adapted fit in the radically different ecosystem they come now to inhabit. Once hemmed in by oceans, these plants play hopscotch because of human travel. These exotics are foreigners, spillovers from civilization. They are like the foreign viruses that land in New York or Los Angeles and upset human health in cities, except that, instead, these upset the health of the land.

Plants do move around on their own. They invade new areas, as when climates change; and one can, if one wishes, speak of naturally invasive species. In prehistoric times, with melting ice, species moved north variously from 200 to

1500 meters per year, as revealed by fossil pollen analysis. Spruce invaded what previously was tundra. Today, most exotic species are introductions that crossed oceans by boat or by air, thousands of times faster than any natural plant movements. Most are rapidly propagating species that arrived in North America within the last 2 centuries. Once on site, exotic species invade typically at a rate of 10 kilometers per year, up to 50 times as fast as the slower natural rates, and upwards of 7 times more than even the faster natural rates. Worse, present and predicted Yellowstone environments will favor exotic species that can shift ranges of latitude, longitude, and elevation at 40–50 times faster than anything observed in the fossil record (Whitlock and Millspaugh 2001).

One way to see the problem is to take *exotic* for a local symbol of ongoing global events. Look forward a century. Michael Soulé says:

> In 2100, entire biotas will have been assembled from (1) remnant and reintroduced natives, (2) partly or completely engineered species, and (3) introduced (exotic) species. The term *natural* will disappear from our working vocabulary. The term is already meaningless in most parts of the world because anthropogenic [activities] have been changing the physical and biological environment for centuries, if not millennia (1989:301).

That forces us to ask whether we want an entirely managed nature, where humans engineer and assemble the biotas, or disassemble them by ignorance and accident, a landscape where nature has come to an end.

4. PRISTINE NATURE

These lines of argument converge with the claim that the quest for pristine nature is a hopeless quest, whether past, present, or future. Humans are always around, Europeans now and earlier the Native Americans. Humans are the real “exotics.” On every continent except Africa, humans are foreigners out of place, and everywhere, Africa included, they have long since displaced the native vegetation.

Just what wild nature was present in the Americas before the Native Americans arrived 15,000 years ago cannot be known. Even if it could be known, that was Pleistocene nature. Climates have since changed; and nature today, had it been left on its own, would be vastly different from any Pleistocene nature. So the quest for pristine nature out of the past is a hopeless quest—so that argument goes. All we have, or have ever had, is a dynamically changing nature occupied by humans.

The quest for pristine nature today is even more hopeless—and now the argument takes a new turn. The very idea of some humanless nature separates humans from nature, falsely. We have contaminated every landscape we observe, if not by our hands with our tools, then by our minds with our cultural baggage. Edwin Dobb summarizes this view:

> Any definition of nature that excludes people and their works has always been indefensible, as has any definition of humanity that excludes nature. Wherever we stand, in the Gila Wilderness or in Times Square, we stand at the intersection of nature and culture (1992:46).

By this logic, both Yellowstone and Times Square are intersecting nature and culture. At Times Square modern Americans intersect nature, having rebuilt it dramatically there. In Yellowstone, too, first the Native Americans intersected nature on their hunts, and today the tourists intersect nature as place of vacation. No human ever knows any nature without intersecting with it.

But this is indiscriminate. Nature, as it existed for millennia before people and their works arrived, is quite a defensible definition of nature. When “we” stand in the Gila or the Absaroka Wilderness, there is an intersection of the nature I behold and the cultural education with which I behold it. But when I am no longer standing there, there is a Gila and an Absaroka Wilderness in which people and their works are, if not entirely absent, insignificant on the landscape beheld. Experiencing the Gila Wilderness, Dobb reconsiders: “There is something that lies beyond the reach of culture” (1992:50). To fail to discriminate between the relative proportions of nature and culture in the Gila Wilderness and in Times Square only glosses over important issues about which we are concerned both in understanding our human place in nature and in our responsibilities for its conservation.

Sometimes one encounters the objection that the slightest human intervention has a sort of totalizing effect and brings straightway the end of nature. This is like saying that the whole moon is pristine no more because the astronauts took a few steps on it, or that the sky is not natural because some jet planes have flown through it. Or that the Absaroka Wilderness is not natural because some aborigines traveled through it once and some backpackers hike there today.

Is it the case that we have lost any possibility of letting Yellowstone be natural? In an absolute sense this is true, since there is no square foot on which humans have not disturbed the predation pressures, nor any on which rain falls without detectable pollutants. But it does not follow that nature has absolutely ended, because it is not absolutely present. Answers come in degrees, with Times Square on one end of a spectrum and the Absaroka Wilderness on another. Events in Yellowstone can remain 99.44% natural on many a square foot, indeed on hundreds of square miles. We can restore nature. We can put the wolves back and clean up the air, and we have recently done both. Wildness can return. Pristine nature is relatively present in the sense (recalling the language of the Wilderness Act) that the dominant ecosystem processes are substantially "untrammeled by man."

This presumes that Yellowstone was wild before the Europeans arrived. But that, it may be protested, underestimates how much Native Americans had already transformed the American landscape. J. Baird Callicott claims:

> Upon the eve of the European landfall, most of temperate North America was not . . . in a wilderness condition—not undominated by the works of man. . . . Most of temperate North America was managed actively by its aboriginal human inhabitants. In addition to domesticating and cultivating an extraordinarily wide range of food and medicine plants, native North Americans managed the continent's forest and savannah communities, principally with fire. . . . The European immigrants, in fact, found a man-made landscape, but they thought it was a wilderness because it didn't look like the man-made landscape that they had left behind (1991: 241).

So pristine nature is a bad idea, because there isn't any.

Whether this is so is, in part, an ecological question whether ecosystems were so thrown out of balance that no wild nature remained. In part, this is an anthropological question concerning the practices of the pre-Columbian peoples. The question is to be answered by historical records, so far as these exist, and by scientific analysis of the extent of altered ecosystems. Philosophers have no particular competence here about the empirical facts, but they can analyze how these facts are incorporated into arguments to see whether the conclusions reached plausibly follow.

Neither the Wilderness Act nor meaningful wilderness designation requires that no humans have ever been present, only that any such peoples have left the lands "untrammeled." The land yet "retains its primeval character and influence." Paul Schullery, a recognized Yellowstone authority, first answers the question this way: Yellowstone's "discovery" by whites followed 10,000 years of occupation and use by Native Americans, and the Native Americans were "very aggressive land managers." But he goes on to quote Philetus Norris, the park's 2nd superintendent and an archaeologist, who noticed how rapidly the Indian remains faded away, concluding that "these Indians have left fewer enduring evidences of their occupancy than the beaver, badger, and other animals on which they subsisted." Schullery adds, "In a sense, he was right" (1997:11–12). The Indian presence was not that exotic; it has faded away and nature has returned.

The only Indian practice that might have extensively modified the Yellowstone landscape is fire. Fire is also quite natural. Forests in the Americas have been fire adapted for at least 13 million years, since the Miocene Epoch of the Tertiary Period, as evidenced by fossil charcoal deposits. The fire process involves fuel buildup over decades, ignition, and subsequent burning for days or weeks; any or all of the 3 may be natural or unnatural. Fire suppression is unnatural and can result in unnatural fuel buildup, but no one argues that the Indians used that as a management tool, nor did they have much capacity for suppression. The argument is that they deliberately set fires. Does this make their fires radically different from natural fires?

It does in terms of the source of ignition; the one is a result of environmental policy deliberation, the other of a lightning bolt. But students of fire behavior realize that in dealing with forest ecosystems on regional scales, the source of ignition is not a particularly critical factor. Once the fire has burned 100 yards, the vegetation cannot tell what the source of ignition was. The question is whether the forest is ready to burn, whether there is sufficient ground fuel to sustain the fire, whether the trees are diseased, how much duff there is, and so on. If conditions are not right, it will be difficult to get a big fire going; it will soon burn out. If conditions are right, a human can start a regional fire this year. If not, lightning will start it next year, or the year after that.

In forests natural ignition sources are available on an order of magnitude (a few years) that greatly exceeds the order of magnitude of fuel buildup for burning (several decades). A. Starker Leopold put it this way:

> If the area is ready to burn, it makes little difference . . . whether the fire is set by lightning, by an Indian, or by [a park scientist], . . . so long as the result approximates the goal of perpetuating a natural community" (quoted in Lotan et al. 1985:65).

It is difficult to make the case that Native American fires in Yellowstone, centuries ago, so dramatically and irreversibly altered the natural fire regime that it is impossible to find meaningful wildness there today.

Most of what we think of today in the United States as pristine nature, much of that which we have designated as wilderness areas or parks, was infrequently used by the aborigines, since such areas are often high, cold, arid mountains or canyonlands difficult to traverse on foot. There the Indians were seasonal or transient hunters—for the same reasons that the whites after them left those regions sparsely settled. In places such as Yellowstone, the Native Americans were "visitors who did not remain."

Just what did these Native Americans do to manage the Grand Canyon, or Mount Rainier? Or Yellowstone or, for that matter, the Great Smoky Mountains? Or regional wetlands such as the Everglades? Is there any designated wilderness in which, on regional scales, the fundamental ecosystemic processes today are recognizably different from what they would have been had there been no Native Americans? That is a question for scientists to answer, not philosophers. But, having posed that question repeatedly to various ecologists, I have not yet identified such an ecosystem.

5. MANAGED NATURE AND NATURE AT AN END?

But now my critics will retort: You are suffering from double illusion. Not only are you deceived about the past; you are deceived about the present. Even though the public still equates national parks with primordial, untouched wilderness, the reality is considerably different. The very appearance and design of national parks is based on social conventions, for example, aesthetic and political ideologies, that allow "land" to become "landscape." Ethan Carr claims:

> The designed landscapes in national and state parks, as works of art, directly express the value society invests in preserving and appreciating natural areas. Few other arts, with the exception of landscape painting, more fully explore this leitmotif of American culture. Neither pure wilderness nor mere artifact, the national park is the purest manifestation of the peculiarly American genius which sought to reconcile a people obsessed with progress with the unmatched price paid for that advance: the near total loss of the North American wilderness (1998:9).

We hire forest managers and park interpreters to teach us about nature in contrast to culture. But the nature-in-contrast-with-culture view is the epitome of social constructs, made in a self-consciously technological society. In reality, there is no nature-culture dualism; this is an artifact of the eyeglasses Westerners wear when they look at nature.

One way to ask whether what we see in Yellowstone is what our managers teach us to see, this recently constructed American nature-other-than-culture, is to ask: Is this National Park Service distinction between nature and culture only Western and modern? Or is some such distinction transcultural?

In a 12th-century poem, *The Owl and the Nightingale,* the poet remarks, "Their land . . . isn't civilized, rather it is a wilderness (*wildernisse*)" (Dickins and Wilson 1951:54, line 95). In Greece, Plato claims this as "the wisest of all doctrines: that all things do become, have become, and will become, some by nature, some by art, and some by chance" (Laws, 10.888). In the Bible the Hebrews regularly distinguish between their own activities and those of wild nature, especially in Job and the Psalms. The word *wilderness* occurs over 300 times in the Bible. The Chinese anciently distinguished between nature and culture, a distinction found in the Analects of Confucius.

In fact, in an etymological study of the word *nature,* C.S. Lewis concludes:

> This, as it is one of the oldest, is one of the hardiest senses of *nature* or *natural.* The nature of anything, its original, innate character, its spontaneous behaviour, can be contrasted with what it is made to be or do by some external agency. A yew-tree is *natural* before the topiatrist has carved it. . . . This distinction between the uninterfered with and the interfered with . . . [is] very primitive. . . . What keeps the contrast alive . . . is the daily experience of men as practical, not speculative beings, [such as] the antithesis between unreclaimed land and the cleared, drained, fenced, ploughed, sown, and weeded field (1967:45).

Every culture can, to some extent, see beyond itself to a spontaneous nature, unaffected by human agency. The very idea of culture, in any form, has the sense of cultivation, of taking oversight, direction, and control of a found natural process to redirect it. That contrast is found wherever there are people with minds and hands who act on the world to alter it, revising the course of events that might naturally have taken place.

Now it seems that the main idea in nature is that the natural is not a human construct. Intentional, ideological construction is exactly what natural entities do not have; if they had it, they would be artifacts. The main idea in nature is that nature is not our idea. If so, why cannot Yellowstone park interpreters, contrary to Carr's claim, so "design" the visitor's experience as to facilitate the discovery of nature in, with, and under culture, of pristine nature yet present on this relatively wild landscape?

Maybe there can be some reasonable illusion of a once primitive nature in Yellowstone, like a museum piece on the landscape. But now a new protest arises. This is backward looking, because such landscapes are vanishing. Agreeing with Michael Soulé, only now enthusiastically endorsing the changes, Daniel Botkin says: "Nature in the twenty-first century will be a nature that we make. . . . We have the power to mold nature into what we want it to be" (1990:192–193). Of course he, like many others, urges us "to manage nature wisely and prudently"; and, to that end, ecology can "instrument the cockpit of the biosphere" (1990:200–201). That sounds like high-tech engineering which brings wild nature under our control, remolding it into an airplane that we fly where we please.

So, it does seem possible to end nature by transforming it into something humanized. This has already been taking place, and the future promises more, at an escalating pace. Over great stretches of Earth, wild nature already has been or likely will be diminished in favor of civilization. Wild nature will never again be the dominant determinant of what takes place on inhabited landscapes.

What is the role of Yellowstone in such a century of managed nature? Perhaps, the park interpreters are looking backward, nostalgic about a past that we really no longer have. Yellowstone is quaint: a tiny corner of a continental landscape mostly managed for multiple uses, this little bit being intentionally managed to create an illusion of wild nature. But really, nature is at an end, as the rest of the landscape demonstrates. There is evidence for this even in the park. Those exotics prove that all we can have is nature modified by the human presence. Even if we set policy to remove the exotics, we will still, for all that, have managed nature, in this case, managed to minimize the exotics. The final philosophical lesson is that wild nature is gone; the new millennium is one of humans managing the Earth.

But for Yellowstone to accept such museum status would be a great mistake. Why? Because nature is always still present and potentially active. Natural forces will flush out many human effects, similarly to the way in which natural effects themselves also are often washed out. Indeed, some human impacts on nature are quite ephemeral. Hiking through a forest after a snow, one leaves Vibram sole bootprints, which are unnatural artifacts contrasted with the tracks of the rabbits. But the snow soon melts, and both sets of tracks are gone.

Humans intervene; but, withdraw the humans, and natural forces return and obliterate the human effects. Wagon tracks of the pioneers in the American West remain, in some locations, a century and a half later. But nature heals these scars; nature comes back. "As for man, his days are like grass; he flourishes like a flower of the field; for the wind passes over it, and it is gone, and its place knows it no more" (Psalm 103.15). These ancient words come to mind when one is standing at the last traces of a pioneer homestead, long since abandoned, and now so reclaimed by nature that, were it not for a few rocks from the collapsed chimney, it would be difficult to tell where the house stood. One sometimes wishes to pack out the trash; but, in other moods, there is something moving about leaving the old cans and watching what nature does with them. Here we need for ourselves the lesson we learned about the Native Americans. When Europeans too draw back, nature comes back, perpetually present. Yellowstone interpreters need to teach that, not that nature was once upon a time here and is now gone.

6. YELLOWSTONE NATURE AS AN END IN ITSELF

Nature neither is, nor ought to be, ended. Rather, humans can and ought to make nature an end in itself, complementary to their own human ends. We do not want entirely to transform the natural into the cultural, nor do we want entirely to blend the cultural into the natural. Neither realm ought to be reduced to, or homogenized with, the other. Otherness is not, ipso facto, a bad thing. We do not want a humanized nature, shore to shore, ocean to ocean, pole to pole. Humanizing it all does not make us a part of it; rather, the dominant species becomes still more dominant by managing all. That, ipso facto, sets us apart: the one species that manages the place.

Rather, we humans, dominant though we are, want to be a part of something bigger; and this we can only do by sometimes drawing back to let others be. This we do precisely by recognizing the otherness of wildness, by setting aside places such as Yellowstone as sanctuaries and wilderness where we will not remain, which we will not trammel. Insisting on being part of everything, even wilderness, separates us out just because nothing else on earth so insists.

Wildness is a place where humanity is absent, not completely, but nearly enough to allow independence. Humans need to see their lives in a larger context, as embedded in, surrounded by, evolved out of a sphere of natural creativity that is bigger than we are. Humans who cannot do this never know who they are and where they are; they live under some other and inadequate mythology. In that sense, it is important that this nature is independent of humans. Setting aside wild places, fauna and flora, as ends in themselves will do two good things. It will respect the intrinsic value in such pristine nature. It will conserve places on the planet where humans, when they visit there, can experience their lives in this larger context. Either of these benefits is sufficient reason for saving nature as an end in itself.

Yes, there is a sense in which Yellowstone Park, so designated by the U.S. Congress, is an artifact of American culture. Perhaps it is necessary to manage Yellowstone so as to restore wildness, for instance, to minimize or remove the exotics. But we ought not to be so easily led to think there is no wild nature on the Yellowstone landscape, yes, even pristine nature. That is what tourists come to Yellowstone to see. Make Yellowstone, as it was founded to be, "a pleasuring-ground for the benefit and enjoyment of the people" (U.S. Congress 1872). Better still, let this be a place where people encounter wild nature and take pleasure in it. Teach them that nature is the ground of culture, that culture transcends nature, that humans emerge from nature. But teach them too that nature is a womb that humans never entirely leave.

Nature can do much without culture—the several billion years of evolutionary history are proof of that. Culture, appearing late in natural history, can do nothing without nature as its ground. To use a word in some disfavor, in this *foundational* sense, nature is the given. To take a favored word and turn it on its head, rather than culture *constituting* nature, nature here is *constitutional* for culture. No culture can ever be independent of nature. Culture will always have to be constructed (constituted) out of nature.

Let Yellowstone teach, in conclusion, that nature is forever lingering around. There is a sense in which nature has not ended and never will. Humans depend on nature for their life support. Humans use nature resourcefully, modifying and rebuilding it in their cultures. Humans stave off natural forces, but the natural forces can and will return, if one takes away the humans. Let Yellowstone be the place that Americans can forever encounter once and future nature.

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EFFECTS OF EXOTIC SPECIES ON YELLOWSTONE'S GRIZZLY BEARS

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ABSTRACT.—Humans have affected grizzly bears (*Ursus arctos horribilis*) by direct mortality, competition for space and resources, and introduction of exotic species. Exotic organisms that have affected grizzly bears in the Greater Yellowstone Area include common dandelion (*Taraxacum officinale*), nonnative clovers (*Trifolium* spp.), domesticated livestock, bovine brucellosis (*Brucella abortus*), lake trout (*Salvelinus namaycush*), and white pine blister rust (*Cronartium ribicola*). Some bears consume substantial amounts of dandelion and clover. However, these exotic foods provide little digested energy compared to higher-quality bear foods. Domestic livestock are of greater energetic value, but use of this food by bears often leads to conflicts with humans and subsequent increases in bear mortality. Lake trout, blister rust, and brucellosis diminish grizzly bears foods. Lake trout prey on native cutthroat trout (*Oncorhynchus clarkii*) in Yellowstone Lake; white pine blister rust has the potential to destroy native whitebark pine (*Pinus albicaulis*) stands; and management response to bovine brucellosis, a disease found in the Yellowstone bison (*Bison bison*) and elk (*Cervus elaphus*), could reduce populations of these 2 species. Exotic species will likely cause more harm than good for Yellowstone grizzly bears. Managers have few options to mitigate or contain the impacts of exotics on Yellowstone's grizzly bears. Moreover, their potential negative impacts have only begun to unfold. Exotic species may lead to the loss of substantial high-quality grizzly bear foods, including much of the bison, trout, and pine seeds that Yellowstone grizzly bears currently depend upon.

Key words: exotic species, grizzly bears, Yellowstone, Ursus arctos, *white pine blister rust, brucellosis, lake trout, clover, dandelion.*

Grizzly bears (*Ursus arctos horribilis*) in the contiguous United States were extirpated from 98% of their historical range between 1850 and 1950 by human-caused mortality, often precipitated by competition for space and resources (U.S. Fish and Wildlife Service 1993). The Greater Yellowstone Area (GYA) contains 1 of the 2 largest remaining grizzly bear populations in the contiguous United States, in an area of about 23,000 km^2. Grizzly bears in this region were listed as threatened under the U.S. Endangered Species Act in 1975 for several reasons, including "the present or threatened destruction, modification, or curtailment of habitat or range" (U.S. Fish and Wildlife Service 1993). In the GYA, deleterious human influences persist in the form of human developments, roads and trails, direct mortality, loss of secure habitat, and availability of human foods. Humans also have affected grizzly bears by introducing exotic or nonnative species.

Yellowstone's grizzly bears have coexisted with exotic species for decades. However, the spread of exotics and their effects on Yellowstone's bears have escalated in recent years. Of all the exotics potentially influencing grizzly bears in the GYA, a select group is notable as being of either the greatest benefit or the greatest harm. This group includes lake trout (*Salvelinus namaycush*), white pine blister rust (*Cronartium ribicola*), domesticated livestock such as cattle and sheep, bovine brucellosis (*Brucella abortus*), common dandelion (*Taraxacum officinale*), and nonnative clovers (*Trifolium* spp.).

In this paper we present an overview of these nonnatives and their current and potential future effects on Yellowstone's grizzly bears. We review and interpret existing relevant information, including published scientific studies and data recently collected by management agencies in the Yellowstone region. We first address nonnatives that are potentially

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important sources of nutrition and then nonnatives that are, directly or indirectly, potentially important threats to bears.

SITE

The Yellowstone grizzly bear population currently occupies over 6 million acres (Fig. 1) in Montana, Idaho, and Wyoming (U.S. Fish and Wildlife Service 1993). This encompasses lands managed by Yellowstone (YNP) and Grand Teton national parks (including the John D. Rockefeller Memorial Parkway) and the Gallatin, Shoshone, Bridger-Teton, Targhee, and Beaverhead national forests as well as some state and private lands (Gunther et al. 1999). Detailed descriptions of the recovery area can be found in U.S. Fish and Wildlife Service (1993, 1994) and Mattson et al. (1991, 1992).

EXOTIC FOODS

Nonnative Clovers and Dandelion

Nonnative clovers and dandelion are widespread in the Yellowstone region. Red and alsike clovers (*Trifolium repens* and *T. hybridum*, respectively) and dandelion arrived in the New World probably along with the first livestock from Europe. Their spread to the GYA was inevitable and was abetted by cultivation of hay in and around YNP, as well as transport of feed into backcountry areas for horses and cattle. There were a surprising number of livestock and haying operations in YNP itself dating back to the late 1800s (Haines 1996, Meagher and Houston 1998). The spread of nonnative clovers and dandelions probably proceeded apace with the well-documented invasion of common timothy (*Phleum pratense*) between the 1880s and 1950s (Houston 1982, Meagher and Houston 1998). More recently, these weedy species have continued to spread on their own along roads and trails aided, in the case of clovers, by the seeding of roadbeds by managers on non-park lands. Even more dramatically, red and alsike clover were broadcast-seeded on U.S. Forest Service lands in the wake of extensive fires during 1988 to stabilize denuded steep slopes and valley bottoms.

Grizzly bears eat dandelion and nonnative clovers wherever these plants are common in grizzly bear range (Mattson 1990). In Yellowstone most consumption of dandelions and clovers by bears occurs between May and August, with use of dandelion peaking earlier (May and June) and use of clover peaking later (July and August). Heaviest grazing of nonnative clovers by bears occurs on dense patches found in low-elevation meadows (Graham 1978, Gunther 1991). Grazing by bears at these sites can be intense enough to maintain a grazing lawn typified by persistent regrowth of succulent foliage stimulated by the heavy cropping. It is not uncommon to find 5 to as many as 50 bear feces at such sites during July. Sites where bears graze dandelions are less well defined, but they are typified by an abundance of dandelions and other forbs (Mattson 2000).

There is no evidence that use of nonnative clovers and dandelion has a population-level effect on either birth or death rates of grizzly bears (Mattson 1998, 2000, Pease and Mattson 1999). As with many other lower-quality foods, however, clover and dandelions can be a substantial source of energy for individual bears for abbreviated periods of time (Graham 1978, Gunther 1991). Overall, the low return of net digested energy obtained from clover and dandelions compared to trout, ungulates, and pine seeds (Mattson et al. 1999) and the generally small fraction of time devoted to grazing these foods (Mattson et al. 1991, Mattson 2000) suggest that population-wide effects on fecundity would be minor.

There is evidence that use of clover, in particular, can lead to elevated conflicts between grizzly bears and humans (unpublished data, Bear Management Office, YNP). This occurs when clover along roads, backcountry trails, or near human developments attracts bears to these areas where they are more likely to encounter humans. Increased exposure to humans can lead bears to lose their fear of man, resulting in an increase of bear-human conflicts and human-caused grizzly bear mortalities (Gunther 1994, Gunther et al. 2000).

To date, there has been little control of nonnative clovers or dandelions by managers of public lands. Managers have often been responsible for the propagation of clover. Compared to other invasive exotic plants that are the focus of management, clovers and dandelions are quite benign. It is unlikely that resources will be allocated for the control of nonnative clovers and dandelion in the near future. Thus, these beneficial exotic foods will likely

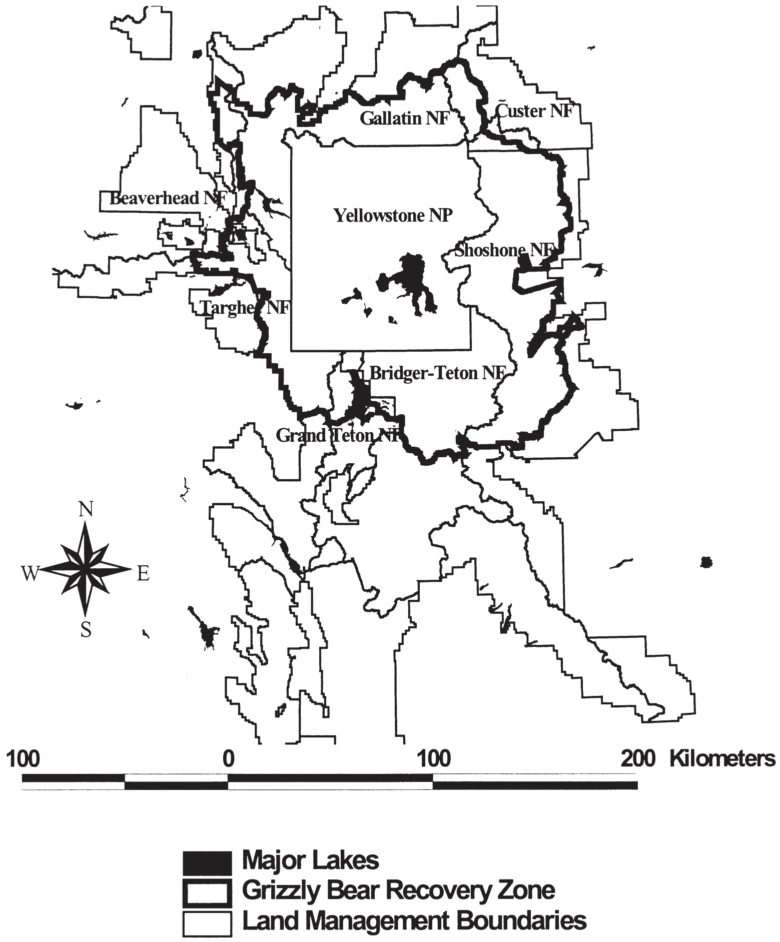

Fig. 1. The Yellowstone Grizzly Bear Recovery Zone on federal lands in the Greater Yellowstone Area.

remain available to bears. However, given local problems with roadside or trailside conflicts arising from grizzly bear use of clover, control of clover in these locations might be considered when secondary negative effects are mitigated and such control is within the scope of governing policies.

Livestock

Grizzly bears prey on domestic cattle, sheep, and occasionally horses in areas where these nonnatives have been introduced into grizzly bear range. Livestock are potentially a high-quality, abundant food source for bears in the GYA. However, livestock also compete with bears for some vegetal foods (Jorgensen 1983, Stivers and Irby 1997), and bears that persistently prey on livestock are usually killed in control actions. Historically, predator control of livestock-depredating carnivores was widespread (Anderson et al. 1997) and contributed significantly to the grizzly bear's decline throughout the western United States (Storer and Tevis 1955, Brown 1985).

In the Yellowstone region most livestock producers winter their livestock on private land, and they then pay a fee to the federal government to graze their livestock on public land (grazing allotment) during the summer season (Mack et al. 1992). There are approximately 392 active grazing allotments encompassing 16,642 km^2 (35%) of public land in the GYA (Mack et al. 1992). Approximately 105,000 sheep, 77,000 cattle, and 1,000 horses (Mack et al. 1992) seasonally occupy these allotments. In comparison, there are an estimated 56,000 elk (*Cervus elaphus*), 6,000 moose (*Alces alces*), and 4,000 bison (*Bison bison*) in the GYA (U.S.

Fish and Wildlife Service 1994). Thus, livestock are potentially both a significant source of nutrition for bears and competitors for vegetal bear foods.

Most grizzly bears will opportunistically prey on livestock (Knight and Judd 1983, Mattson 1990). The majority of grizzly bear depredations on livestock occur from mid- to late June through September while livestock are being grazed on public land (Murie 1948, Jorgensen 1983, Anderson et al. 1997). From 1992 to 1998, of the 301 reported incidents of grizzly bear depredations in the Yellowstone ecosystem, 84% occurred on federal grazing allotments, 15% on private lands, and 1% on state lands (Gunther et al. 1993, 1994, 1995, 1996, 1997, 1998, 1999). Old-age male bears are most likely to become chronic depredators of cattle (Mattson 1990, Anderson et al. 1997).

Livestock are potentially an important source of energy for Yellowstone's grizzly bears. At approximately 4.0–5.5 kcal $\cdot$ g^{-1}, meat from native ungulates and domestic livestock is one of the most concentrated sources of net digestible energy available to bears in the GYA (Mattson et al. 1999). Individual bears can consume numerous cattle or sheep (Anderson et al. 1997). In addition to predation, grizzly bears also scavenge livestock that die from other causes. Even though individual bears may obtain considerable energy from livestock, there is no clear evidence that use of domestic livestock translates into a significant population-level increase in female fecundity (Mattson 2000). Moreover, given that males depredate on livestock more often than females (Anderson et al. 1997), such a population-level effect would be unexpected.

Any positive population-level effect on grizzly bear birth rates is likely negated by the higher death rate of bears that repeatedly kill livestock. Between 1996 and 1999, four grizzly bears involved in livestock depredations were captured and euthanized in control actions. An additional 19 grizzly bears were captured and relocated to areas away from livestock grazing allotments (Gunther et al. 2000); relocated bears typically exhibit higher mortality (Blanchard and Knight 1996). Total livestock-related grizzly bear mortality may be underestimated as some incidents are not reported (Jorgensen 1983).

The number of livestock depredations by grizzly bears in the GYA is increasing (Gunther et al. 2000). Between 1996 and 1999, we documented 265 livestock depredations in the GYA; during 1992–1995 there were 120 depredations (Gunther et al. 2000). Most of the increase in incidents during 1996–1999 occurred outside the designated grizzly bear recovery zone (U.S. Fish and Wildlife Service 1993, Gunther et al. 2000). At present, highly selective control of livestock-depredating grizzly bears has resulted in removal of only the most chronic depredators. Depredation on livestock will likely continue to increase as grizzly bear activity outside the designated recovery zone increases. At some point the level of public tolerance of grizzly bear depredations on livestock will likely be exceeded, especially in areas far from the recovery zone boundary. Predator control actions against depredating grizzly bears will likely increase as well. The interface areas between occupied grizzly bear habitat and livestock-producing agricultural areas are likely to be a continual challenge to grizzly bear managers in the Yellowstone region.

EXOTIC THREATS

Bovine Brucellosis

Bovine brucellosis is a nonnative bacterial disease of ungulates, causing placentitis, metritis, and abortion in newly infected individuals. The precise origin of this disease in North America is not known, but domestic cattle imported from Europe were the likely vector (Meagher and Meyer 1994). Transmission of brucellosis occurs through contact with infected tissue such as aborted fetuses, birth membranes, or vaginal discharges from infectious animals (U.S. National Park Service 2000). Although the disease affects reproduction in wild ungulates, the primary management concern in the GYA is potential transmission from wild ungulates—primarily bison and elk—to domestic cattle. The first known case of brucellosis in Yellowstone bison occurred in 1917 (Meagher and Meyer 1994, U.S. National Park Service 2000). Currently, both bison and elk in the GYA maintain endemic brucellosis.

Carnivores are exposed to brucellosis when preying on infected ungulates or feeding on infected carrion. Blood samples from grizzly bears in the GYA exhibited a 17% (n = 69) seroprevalence to brucellosis, suggesting bears are exposed to the disease through contact with infected ungulates (K. Aune, Montana

Department of Fish, Wildlife and Parks, personal communication). However, there is no evidence the disease negatively impacts reproductive performance in any carnivore. Although the direct effect of brucellosis on grizzly bears is unknown, it is probably negligible. Brucellosis is likely to impact the Yellowstone grizzly bear population indirectly, if reductions in ungulate populations are instituted for disease management.

Until 1968 bison and elk were maintained at low numbers within YNP by direct reductions (Houston 1982). Following termination of this program, numbers of elk and bison and amount of biomass associated with bison and elk increased significantly (Fig. 2; Singer and Mack 1993). Changes in climate during the early 1980s, to drier winters and wetter summers, also may have contributed to this increase (Despain et al. 1986, Engstrom et al. 1991, Balling et al. 1992). For almost 30 years, the YNP bison herd grew steadily, increasing 10-fold by 1996 (U.S. National Park Service 1997). Within the last 2 decades, changes in movements led to increased wintertime use of areas outside YNP by bison (Meagher 1989). These changes in distribution increased the potential for transmission of brucellosis to domestic cattle and brought this issue to the forefront of public and scientific debate.

Planning for control of brucellosis in or near YNP is currently underway (U.S. National Park Service 2000). Interestingly, brucellosis itself is not expected to have an effect on ungulate populations in the Yellowstone region (Meagher and Meyer 1994, U.S. National Park Service 2000). Rather, management of native ungulates to reduce exposure of cattle to the disease may have a greater impact on numbers and distributions of bison. Over 2000 bison were killed between 1994 and 1999 in attempts to limit their movement into agricultural areas (U.S. National Park Service 2000; G. Kurz, YNP, personal communication). Current management plans include the possibility of maintaining bison herds at substantially lower levels than those of the late 1980s. Thus, this disease stands to affect the GYA grizzly population mostly through a management response to the real, or perceived, threat of bovine brucellosis to domestic cattle.

Currently, the GYA supports some of the highest native ungulate densities in North America (Mattson 1997). There was a strong positive relationship between estimated annual standing biomass of ungulates and minimum grizzly bear population estimates (Fig. 2). Although this correlation does not prove cause and effect, it adds further supportive evidence that the availability of ungulates may have a positive influence on the Yellowstone grizzly bear population.

Grizzly bears in the GYA are unique among interior North American populations in their substantial consumption of ungulates (Craighead and Mitchell 1982, Mattson et al. 1991, Mattson 1997). Recently, N_{15} isotopes in grizzly bear hair were used to index the proportion of meat in grizzly bear diets in the GYA (Hildebrand et al. 1999). Findings indicate that ungulate meat comprises almost half of the annual energy intake of adult females and over half for adult males (Hildebrand et al. 1999). Of all ungulate species consumed by grizzly bears, bison are used with disproportionately greatest frequency and intensity, contributing 24% of total ungulate biomass consumed (Green et al. 1997, Mattson 1997). Because ungulates are one of the most concentrated sources of net digestible energy available to Yellowstone's grizzly bears (Mealey 1975, Pritchard and Robbins 1990, Craighead et al. 1995, Mattson et al. 1999), availability of ungulates—especially bison—potentially affects fecundity of the grizzly bear population.

Availability of ungulate meat may influence levels of human-caused grizzly bear mortality. Numbers of bear-human conflicts and human-caused bear mortalities are negatively correlated with availability of high-quality natural foods (Mattson et al. 1992, Gunther et al. 2000). Any significant reduction in ungulate numbers to control the spread of brucellosis may contribute to increases in bear-human conflicts and human-caused grizzly bear mortalities, especially during shortages of other natural foods.

Lake Trout

Yellowstone Lake is home to the largest inland population of native cutthroat trout (*Oncorhynchus clarkii*) in the world. Lake trout were discovered in Yellowstone Lake in 1994. Since then, Yellowstone anglers have caught thousands of lake trout, and tens of thousands have been caught in gill nets set by YNP Aquatic Resources staff (Mahony et al. in preparation). Lake trout are not native to the

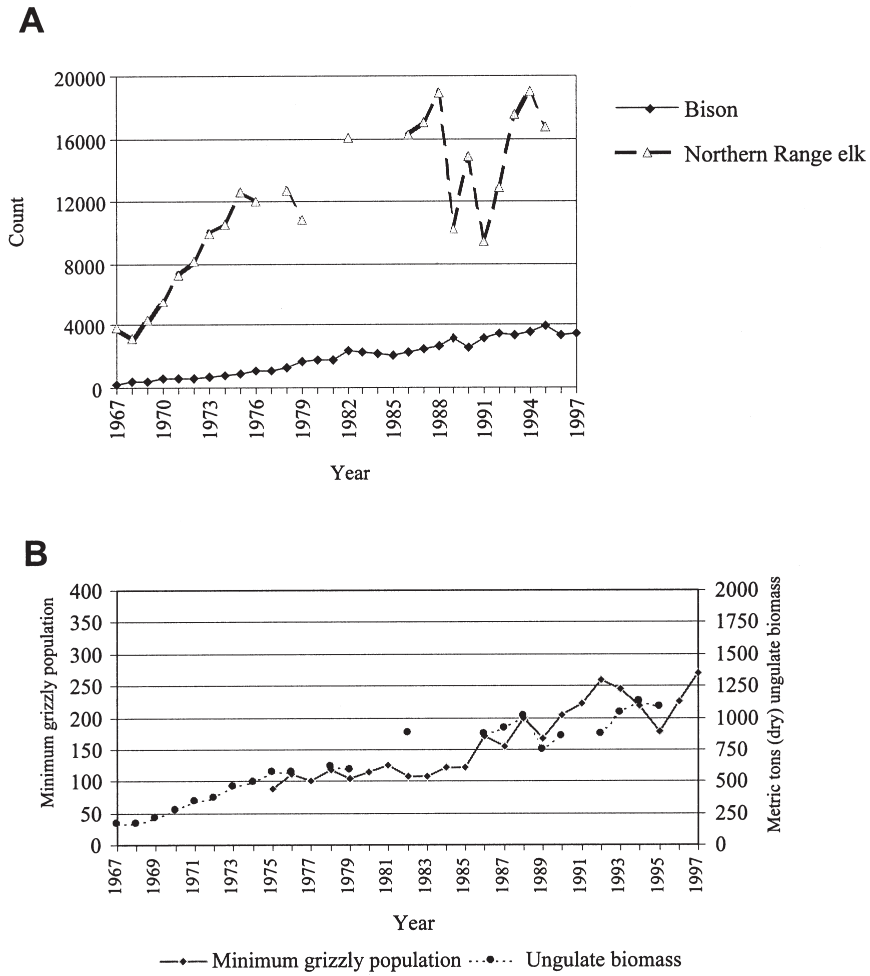

Fig. 2. A, Numbers of bison and northern range elk in YNP, 1967–1997; B, estimated metric tons of standing ungulate (bison and northern range elk) biomass from 1967 to 1997 in Yellowstone National Park. Annual counts of the northern range elk and YNP bison populations are from NPS (1997). Estimates of standing biomass of elk and bison in the Yellowstone ecosystem were calculated using annual ungulate counts, estimated sex and age composition of ungulate populations, and estimates of edible dry weight biomass available from different sex and age classes of elk and bison. Estimates of average sex and age composition for the northern range elk were calculated from Houston (1982). Average sex and age composition estimates for YNP bison were from J. Mack (National Park Service, personal communication) and K. Frey (Montana Fish, Wildlife, and Parks, personal communication). Estimates for dry weight of edible meat available from different sex and age classes of elk and bison were from Mattson (1997). Grizzly bear minimum population estimates and ungulate biomass were positively correlated (*r* = 0.74) between 1975 and 1996 before reductions in bison and wolf reintroduction occurred.

GYA; they were stocked in historically barren Lewis Lake, approximately 7 miles from Yellowstone Lake in 1896. Although the exact origin of lake trout in Yellowstone Lake is not known, they likely came from Lewis Lake. Recent catches of lake trout from Yellowstone Lake revealed a reproducing population, with some 25+-year-old individuals, indicating lake trout have existed in Yellowstone Lake for some time (Mahony et al. in preparation).

Lake trout are major piscivorous predators that threaten to reduce Yellowstone Lake's native cutthroat trout population and adversely affect numerous wildlife species that depend on the cutthroat (Kaeding et al. 1996). The long-term impact of the illegally introduced lake trout on cutthroat trout is potentially substantial (McIntyre 1995, Kaeding et al. 1996, Ruzycki and Beauchamp 1997). Lake trout have reduced native cutthroat trout populations in western North American lakes including Bear Lake, Utah; Lake Tahoe, Nevada; Jackson Lake, Wyoming; and Heart Lake, Yellowstone National Park (Ruzycki and Beauchamp 1997).

Significant reduction of cutthroat trout populations in Yellowstone Lake will alter ecosystem processes, including energy flow to consumers at higher trophic levels. These consumers include 28 known terrestrial and avian species, including grizzly bears (Schullery and Varley 1995). Cutthroat trout are vulnerable to terrestrial and avian predators because they spawn in tributaries and use shallow water within Yellowstone Lake. By contrast, because lake trout primarily use deep waters, they are unavailable to this same suite of predators (Schullery and Varley 1995, Kaeding et al. 1996).

Because of their current abundance, high digestibility, and energy content (Pritchard and Robbins 1990), cutthroat trout are an important part of the diet for numerous grizzly bears (Reinhart and Mattson 1990, Mattson and Reinhart 1995). Despite the limited distribution of fishable cutthroat trout spawning streams, bears from a large portion of the ecosystem likely consume cutthroat trout at some point in their lives (Mattson and Reinhart 1995).

A substantial number of grizzly bears in the GYA are known to use spawning cutthroat trout. Results from a lake-wide survey of all Yellowstone Lake spawning streams during 1987 estimated a minimum of 44 autonomous bears using these streams (Reinhart and Mattson 1990). Analysis of DNA from hair samples collected on selected spawning streams between 1997 and 1999 identified 85 individual grizzly bears (including dependent young) on these streams (Haroldson et al. 2000). This corresponds to approximately 10–30% of the GYA bear population past the age of weaning (Eberhardt and Knight 1996).

Lake trout may already be affecting Yellowstone Lake cutthroat trout abundance. Continued monitoring of front-country cutthroat trout spawning streams near Lake and Grant villages showed a decline in the relative abundance of cutthroat trout from the late 1980s through the mid-1990s. However, in recent years spawning runs have increased to earlier levels on most streams around Yellowstone Lake, but have continued to decline in West Thumb streams (Fig. 3; Haroldson et al. 2000). The decline of spawning cutthroat trout in West Thumb streams may be an early indication of impacts from lake trout. Most lake trout currently occur in the West Thumb area of Yellowstone Lake, despite the removal of thousands by anglers and park managers (Mahony et al. in preparation).

The prognosis for Yellowstone Lake's cutthroat trout is potentially grim. Fisheries biologists have concluded that there is only a slight chance of eliminating lake trout from Yellowstone Lake (McIntyre 1995). They also predict the native cutthroat trout population could be reduced by ≥70% if nothing is done to suppress lake trout. However, there is at least a 50% chance that effective control measures could be instituted (McIntyre 1995). Mechanical measures used by YNP managers to control lake trout include lake-wide gillnetting, capture on spawning grounds, and directed angling. During 1995–2000, catches of lake trout in Yellowstone Lake increased from $200 \cdot \text{year}^{-1}$ to over $13{,}000 \cdot \text{year}^{-1}$ (Mahony et al. in preparation). Yellowstone National Park intends to continue efforts to reduce lake trout numbers and maintain native cutthroat trout populations at levels sufficient to ensure viability and their role as an important ecological component in the GYA.

White Pine Blister Rust

White pine blister rust arrived from Eurasia in North America near Vancouver, British Columbia, in 1910. This fungus infects 5-needled pines and was first noticed in western white pine (*Pinus monticola*) and whitebark pine (*P. albicaulis*) in 1921 and 1926, respectively (Hoff et al. 1994). Of all pines affected by blister rust, whitebark pine is among the least resistant. Over 99% of all trees are susceptible to infection, and of those that become infected, virtually none survive (Hoff et al. 1994). Thus, in areas where blister rust has long been established, almost all whitebark pine are either infected or dead (Kendall 1995). Blister rust spread rapidly south and east and was known from the GYA as early as the 1940s. Following the initial spread, progressive, dramatic losses of whitebark pine to blister rust were documented between the 1960s and the present, especially in areas subject to maritime climatic influences (Keane and Arno 1993, Keane and Morgan 1994, Keane et al. 1994). In the Yellowstone ecosystem, rates of

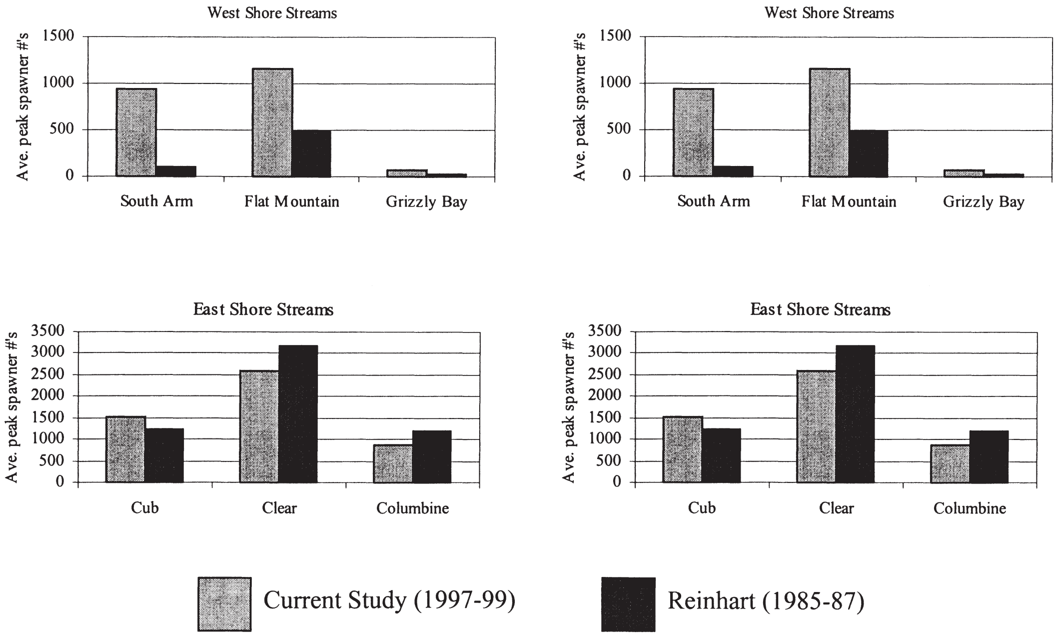

Fig. 3. Comparisons of average peak numbers of spawning cutthroat trout between study periods for 4 different areas of Yellowstone Lake (from Haroldson et al. 2000).

infection have increased from 0–7% in the 1960s to 9–54% in the 1990s, depending on the location (Smith and Hoffman 1998). The prognosis for the future in Yellowstone is inevitable spread of the disease and, along with it, eventual loss of most whitebark pine (Smith and Hoffman 1998, Koteen 1999).

Currently, whitebark pine is abundant in the Yellowstone area. Forests containing mature whitebark pine cover 26% of the landscape (Mattson 2000). Whitebark pine grows to maturity at elevations >2400–2600 m (Mattson and Reinhart 1990). Because of this high-elevation distribution, stands of mature whitebark pine are typically far from most human facilities or places where humans are otherwise active.

Yellowstone's grizzly bears make frequent and substantial use of the large, fatty seeds of whitebark pine (Mattson and Reinhart 1994). During some years pine seeds can comprise the majority of food consumed by bears ecosystem-wide. Consumption peaks during August–October, concurrent with maturation of cones and their harvest by red squirrels (*Tamiasciurus hudsonicus*). This late growing-season period corresponds with hyperphagia—a time of intensive feeding among bears prior to hibernation. Use of whitebark pine seeds by Yellowstone's grizzly bears has substantial effects on their birth and death rates. These benefits result from the energy and nutrients obtained from pine seeds, as well as from the behaviors associated with foraging on this food. Whitebark pine seeds provide substantial concentrations of fat and energy (Mattson et al. 1999) and are used twice as often by female grizzly bears as by males (Mattson 2000). Compared to females that consume few pine seeds, females that use whitebark pine seeds extensively reproduce at an earlier age, produce litters more frequently, and produce more 3-cub litters (Mattson 2000). Death rates of mature grizzly bears also nearly double during years when pine seed crops are small compared to years when they are large (Pease and Mattson 1999). Grizzly bears tend to spend most of their time in remote whitebark pine forests during years when seed crops are large. By contrast, during years when seed crops are small, bears spend much more time at lower elevations, which tend to be nearer human facilities, and consequently experience much more contact and conflict with humans (Mattson et al. 2001) Thus, high-elevation whitebark pine stands act as a refuge where grizzly bears have little contact or conflict with humans (Mattson et al. 1992).

Blister rust is poised to take a major toll on whitebark pine in the GYA. If it does, grizzly bears in the GYA will be negatively affected. With the loss of most whitebark pine, birth rates of grizzly bears will likely decline as death rates increase. Unfortunately, there are no strategies by which the short-term effects of blister rust on whitebark pine can be forestalled. Deliberate or natural selection of blister rust–resistant genomes will be beneficial only over the very long term (Hoff et al. 1994), with success contingent on reestablishment of whitebark pine in areas where it was eliminated. Of all the exotics affecting Yellowstone's grizzly bears, white pine blister rust threatens to be the most damaging.

CONCLUSIONS

Among the exotic species present in the GYA are those of potential benefit and those of potential harm to Yellowstone grizzly bears. However, when viewed in their totality, exotic species have caused or are likely to cause more harm than good. Although important to some bears, clover and dandelion provide little net digested energy compared with bison, trout, and whitebark pine seeds. Clover and dandelion provide about 1.5–2.0 kcal $\cdot$ g^{-1} in contrast to 4.0–5.5 kcal $\cdot$ g^{-1} for bison, 4.5 kcal $\cdot$ g^{-1} for trout, and 2.5 kcal $\cdot$ g^{-1} for pine seeds (Mattson et al. 1999). By contrast, livestock are a concentrated source of energy, similar to bison, and are used by a small proportion of grizzly bears living on the periphery of the GYA and provide a small part of the total meat ingested by Yellowstone's grizzly bears (Mattson et al. 1991, Mattson 1997). Livestock depredations can also lead to removal of bears from the ecosystem and erode public support for grizzly bear conservation. Because of their association with humans or human facilities, exotic foods can increase the frequency of conflicts between grizzly bears and humans, thus leading to deleterious outcomes that likely outweigh energetic benefits to the bear population.

Unfortunately, managers typically have few options to mitigate or contain the impacts of exotics on Yellowstone's grizzly bears. The U.S. National Park Service (NPS) is mandated to prevent the spread and establishment of nonnative species (U.S. National Park Service 1988). Currently, YNP administers programs to monitor and aggressively control lake trout in Yellowstone Lake and noxious weeds throughout the park at a cost of hundreds of thousands of dollars annually (Olliff et al. 2001, Mahony et al. in preparation). There is ongoing research on the use of fire and other silvicultural tools to limit the effects of blister rust in whitebark pine ecosystems (Keane and Arno 2001). However, management strategies focused on nonnative species are costly and of unknown efficacy. Further complications arise in the case of white pine blister rust because management options have been limited by loss to wildfires in 1988 of about 25% of forest stands containing mature whitebark pine in YNP (Renkin and Despain 1992, Mattson et al. 2000).

Ungulate meat may become even more important to the nutritional well being of Yellowstone's grizzly bears if whitebark pine seeds and cutthroat trout are reduced by introduced exotics. The NPS is developing plans to manage brucellosis (U.S. National Park Service 2000). Unfortunately, the effects on grizzly bears of various proposals to control brucellosis have not yet been rigorously examined. Any programs that reduce ungulate numbers will likely exacerbate the effects of whitebark pine and cutthroat trout declines. Short-term bear-human conflicts and related human-caused grizzly bear mortalities will likely increase, especially during years when natural bear foods are in short supply. Long-term reproductive success will be reduced because of older age of first reproduction, longer between-litter intervals, decreased litter size, and lower cub survival (Boyce et al. 2000, Mattson 2000). In essence, the grizzly bear population will likely exhibit characteristics of a nutritionally stressed population similar to those observed a decade following the closure of the open pit garbage dumps in 1972 (Craighead et al. 1995).

We have focused on a few exotic organisms, but others could affect Yellowstone grizzly bear habitat and foraging opportunities. Noxious weeds can impact ecosystem processes, leading to changes in native plant community structure and distribution as well as foraging and abundance of ungulate and small mammal populations (Kurz 1995, Trammel and Butler 1995, Thompson 1996). In aquatic systems recent findings of New Zealand mudsnails (*Potamopyrgus antipodarum*) and whirling disease (*Myxobolus cerebralis*) in the Yellowstone drainage (Mahony et al. in preparation) may further reduce native cutthroat trout abundance. Additional exotics with the potential to affect bears may be present in the GYA, or they could arrive in the near future and have not yet been identified.

The most troubling aspect of exotic species, especially with respect to bears, is that their potential negative impacts have only begun to unfold. At best, exotic organisms increase the uncertainty of any projection for Yellowstone's grizzly bear population. At worst, exotics could lead to declines in carrying capacity, fecundity, and overall resilience to long-term stressors. Certainly, the potential effects of exotics need to be considered in long-term planning for conservation of the Yellowstone grizzly bear population.

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MOUNTAIN GOATS IN THE GREATER YELLOWSTONE ECOSYSTEM: A PREHISTORIC AND HISTORICAL CONTEXT

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ABSTRACT.—Because the relatively recent colonization of portions of Yellowstone National Park by introduced mountain goats (*Oreamnos americanus*) from public game lands in Montana raises important policy and management questions for the park, it is necessary to understand the prehistoric and early historical record of mountain goats in the Greater Yellowstone Ecosystem. We reviewed previous paleontological, archeological, and historical studies of goat presence and examined a large body of historical material for evidence of goats. Native mountain goat range most closely approached the Greater Yellowstone Ecosystem to the west, but no modern authority claims goats were resident in the ecosystem in recent centuries. Historical accounts of goat presence in the region prior to 1882 (and thus prior to any known introduction of goats by Euro-Americans) are limited to one possible sighting by unreliable observers and a few casual mentions of goat presence by people of limited or unknown familiarity with the ecosystem. Other early observers in the region specifically stated that goats were not native. Between 1882 and 1926 other observers and residents agreed that mountain goats were not native to the park, or to the larger area around it. It is impossible to prove absolutely that there were no goats in the ecosystem prior to modern introductions, but historical evidence demonstrates that if present, such goats must have been exceedingly rare and uncharacteristically unsightable. National Park Service policy relating to exotic species developed gradually after the creation of Yellowstone National Park in 1872, moving from a general receptivity to introduction of at least some favored nonnative species to a general prohibition on all such introductions. Current policy, while disapproving of all nonnative species, seems to reserve special efforts at removal of nonnatives for those species that pose the greatest threat to native species and ecosystems. Current policy is not helpful in defining the minimum amount of evidence needed to prove a species was present or absent, or whether or not an introduced nonnative species is causing sufficient harm to justify its removal.

Key words: mountain goat, nonnative species, National Park Service policy, Yellowstone National Park, Greater Yellowstone Ecosystem, ecological historiography.

This paper will summarize the historical record of mountain goats in the Greater Yellowstone Ecosystem (GYE) and then will review the development of National Park Service (NPS) policy relating to exotic species. Finally, it will consider current goat colonization of the park in light of history and policy.

It seems especially appropriate, even if entirely accidental, that Yellowstone National Park (YNP) hosted a conference on nonnative species over Columbus Day weekend in October 1999. It has become a standard practice, almost a cultural act, among those concerned with the health of native ecosystems, to divide the history of the New World at a point that is our own equivalent of B.C.—Before Columbus. The enormously complex and breathtakingly swift overhaul of the North American landscape that has occurred since 1492 is now such a fact of life that most Americans give it little thought and may not even be aware of its magnitude. In modern Montana, for example, the public depends upon the enjoyment or employment of brown trout (*Salmo trutta*), pheasants (*Phasianus colchicus*), horses (*Equus caballus*), cattle (*Bos taurus*), and many other species of animals and plants from other continents. Most of these species are deeply embedded in the national consciousness as constituting part of the "traditional" western scene.

Of course, the mountain goat is different: it is native to North America. Euro-American influences have not been confined to bringing new species to this continent. We have also transported native species long distances around the continent. Mountain goats in YNP provide an excellent case study of the complexities of issues relating to nonnative species in national parks.

Because the boundaries of YNP are largely artificial and reflect little regard for ecological

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realities, we will address the question of mountain goat prehistory and early history from the broader and slightly less artificial perspective of the entire Greater Yellowstone Ecosystem (GYE; Fig. 1), using recent definitions of it as an area upwards of 20 million acres encompassing the highlands in and around Yellowstone and Grand Teton national parks (Glick et al. 1991).

The prevailing scientific consensus is that native mountain goat populations existed most closely to the west of the GYE, in central Idaho along the Idaho-Montana border (Rideout 1978, Chadwick 1983, Laundré 1990). Perhaps the most popular contemporary definition of the GYE, proposed by the conservation group known as the Greater Yellowstone Coalition (Glick et al. 1991), places its western boundary somewhat short of that historic native goat range, perhaps less than 50 miles (imprecision is the result of vagueness of current definitions of GYE boundaries).

ISSUES OF EVIDENCE

The search for evidence that may not exist is one of historical scholarship's most interesting enterprises because investigators run the risk of committing what Fischer (1970) describes as the "fallacy of the negative proof":

> It occurs whenever a historian declares that "there is no evidence that X is the case," and then proceeds to affirm or assume that not-X is the case. . . . [A] simple statement that "there is no evidence of X" means precisely what it says—no evidence. The only correct empirical procedure is to find affirmative evidence of not-X—which is often difficult, but never in my experience impossible (Fischer 1970:47).

In the case of mountain goats in the GYE, we suspect that Fischer would be faced with difficulty in describing for us "affirmative evidence of not-X." It appears that it will be extremely challenging to establish an unequivocal affirmative proof that absolutely no mountain goats inhabited the GYE prior to the arrival of Euro-Americans. We also believe that our study has provided an interesting test of the concept of negative evidence, a test that we will discuss later.

But Fischer's point about negative evidence is very important in the question of mountain goats in the GYE. Paleontology, archeology, and history are more successful at establishing that a species *was* native than at proving that it was *not.* The prehistoric and historical evidence is always assumed to be incomplete. Even if it provides no indication a species was present, we are always left with at least a lingering uncertainty because negative evidence can always be overridden later by new positive evidence. The next paleontological investigation, the next archeological dig, or the next newly discovered early trapper's journal may yield suggestive or conclusive evidence that the species in question was here after all.

Several reasons have been suggested for possible underrepresentation of mountain goats in a survey of archeological and paleontological sites (Laundré 1990, Hutchins 1995, Lyman 1998). The use of evidence from such sites to determine presence or abundance of a given species in past times is fraught with difficulties (Grayson 1981), including the following:

1. Even if mountain goats have fully occupied the available habitat in a region, they will probably be neither as numerous nor as accessible to hunters as other ungulate species and thus may not be harvested as often, thereby not finding their way into archeological sites as frequently as other species might.
2. Living as they do in steep country, when they die their remains may fall considerable distances and be scattered rather than find their way into paleontological sites (e.g., packrat middens).
3. If most archeological and paleontological investigations are conducted at lower elevations, they may include only, or primarily, lower-elevation species.
4. The native people who occupied the site and left animal bones there were operating under unknown cultural systems, with now incompletely understood attitudes and preferences relating to which animals they killed and which they did not; they certainly would prefer some species over others, thus introducing a bias into what their archeological sites "collect" for us to study.
5. Last, even an identifiable piece of bone or horn from a mountain goat may in some cases not be proof the animal lived in the immediate vicinity of the site in which it was found. If the bone or horn had potential value (for example, as a tool or ceremonial device), it might have been carried a considerable distance to the site.

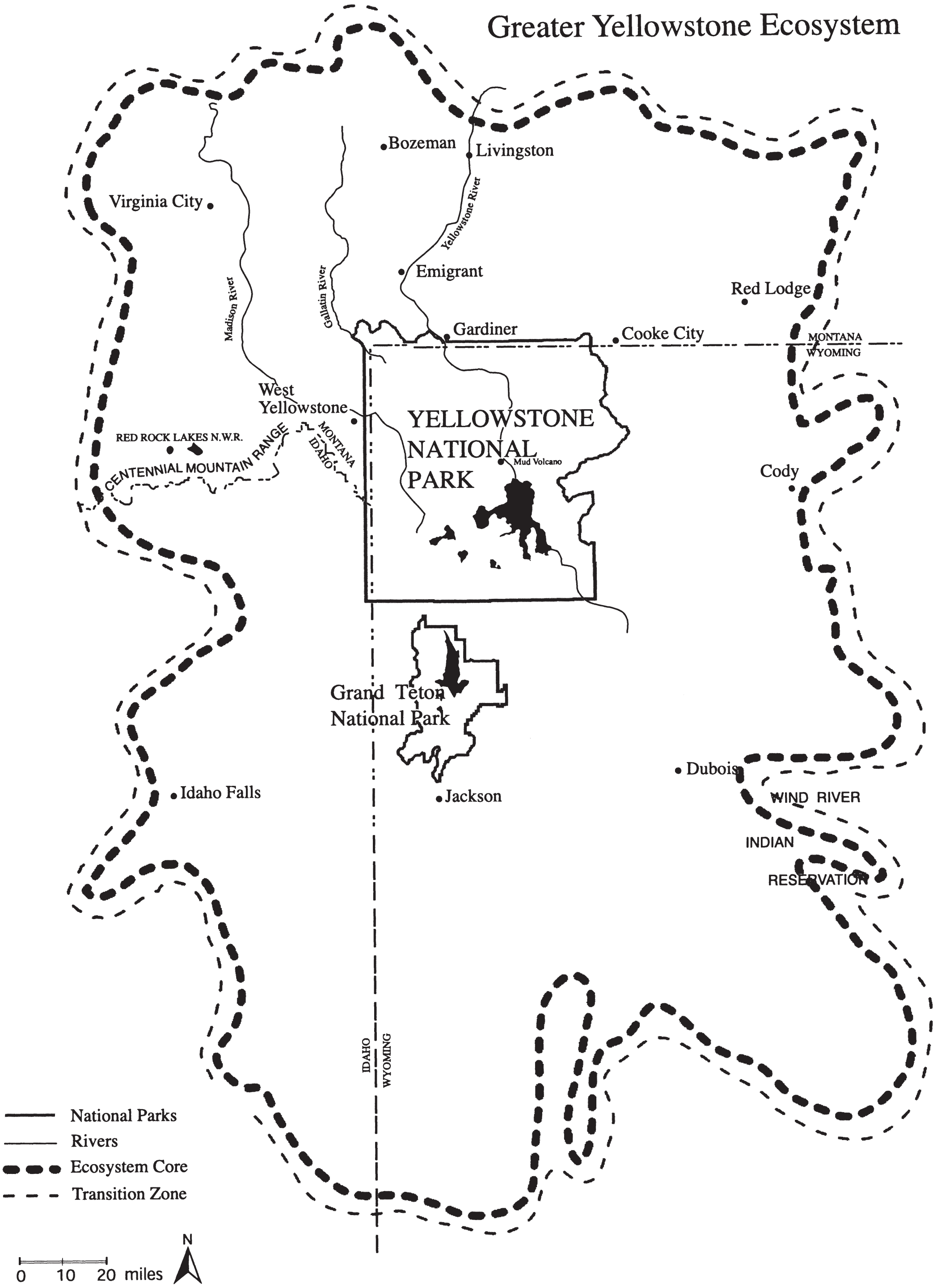

Fig. 1. The Greater Yellowstone Ecosystem. Figure by Renée Evanoff.

Another potentially useful kind of evidence of pre–Euro-American wildlife conditions is provided by rock art: pictographs and petroglyphs. These are sometimes problematic as well. A rock-art image does not necessarily prove that the animal represented lived nearby. Often it is difficult or impossible to identify the species depicted; sometimes the animal shown was not a "real" species but the product of visions that are closely associated with rock art in the region. Species represented in rock art in our region tended to have a set of cultural values unlike species preferred for food (J. Francis personal communication). Still, like other archeological as well as paleontological evidence, rock art images provide a potentially useful information source.

Written historical accounts likewise present researchers with a variety of obstacles. Accounts are often hard to locate or may not exist for all localities. Writers of early accounts were often of unknown education, familiarity with wildlife, and bias. These writers tend to exhibit preferences for topics depending upon personal interests; these preferences, while not predictable for each individual, can be gauged for certain types of observers. As a general rule, for example, commercial trappers emphasized fur-bearing animals and habitats in their written accounts. On the other hand, some wildlife species, such as grizzly bears (*Ursus arctos*), were of at least some interest to many types of travelers, probably because of their greater threat or their formidable presence in most northern human cultural traditions. From yet another perspective, very few early writers, of any persuasion, bothered to mention small mammals. Early visitors to YNP had still another bias introduced into their narratives: the park's primary attraction was its geothermal activity. YNP visitors, though many did hunt in the park during its first 11 years, were here primarily to see the famous geological oddities. Wildlife did not become an important visitor attraction as an object of touristic attention (i.e., wildlife watching as recreation) until the later 1880s and 1890s (Schullery 1997).

It has also been pointed out that even in the earliest period of Euro-American visitation of lands that would eventually become national parks in the northern Rockies, roughly 1800–1880, various influences of Euro-Americans on the landscape—such as the effects of European diseases on numbers and activities of native people; the adoption of the horse, firearms, and other iron tools by native people; and European livestock diseases—were all potentially at work affecting the landscape. Such effects may or may not have been pronounced enough to significantly alter plant or animal communities from their earlier appearance, but if they were, the first white observers would have been describing a landscape not entirely free of their own culture's effects (Schullery 1984, 1997, Kay 1994).

Terminology is often treacherous in early historical accounts. For example, in some western 19th-century accounts, coyotes were known as "prairie wolves." Black bears (*Ursus americanus*) were sometimes called "cinnamon" bears depending upon their color, but a cinnamon- or brown-colored bear might be a misidentified grizzly bear; and, of course, a black-colored grizzly bear might simply be described as a "black bear" with no intention of indicating species. Early 19th-century writers sometimes referred to elk as red deer, their European name. And quite a few early writers on the West, including some who traveled through the GYE, referred to pronghorn (*Antilocapra americana*) as "goats" (e.g., Stuart 1935, Lewis and Clark 1987). Casual use of other terms could complicate the problem, as when a writer referred to a "buck" but meant a "bull" elk (*Cervus elaphus*). Careful reading of the material and close attention to the context can settle many such confusions, but some are almost irresolvable and are always complicated by observer ignorance as well as *our* ignorance of just how well informed the observer might have been.

We do not wish to cast so much doubt on paleontological, archeological, and historical evidence as to suggest that these sources of information are valueless. They may be the best tools we have, and they are often excellent tools indeed. It is our experience, however, that the tools must be used with great care and discretion if they are to serve our needs.

PALEONTOLOGICAL AND ARCHEOLOGICAL EVIDENCE OF MOUNTAIN GOATS

Love (1972) conducted an archeological survey and historical literature review of the Jackson Hole region, and, though he discussed all other relevant large mammals, he mentioned no mountain goats in either record. We assume this is because he found none. Cannon (1992) reviewed archeological and paleontological evidence for the northern and central Rockies physiographic provinces, including 31 late-Pleistocene–Holocene sites in northwestern Wyoming, southern and western Montana, and near the Idaho-Wyoming and Idaho-Montana borders in Idaho. No mountain goats were reported in any of these sites. It is interesting that 2 of the Idaho sites he reviewed, Veratic Rockshelter and Jaguar Cave, are relatively close to areas known to have been native mountain goat habitat along the Idaho-Montana border. Laundré (1990) also reviewed paleontological and archeological reports from the GYE and found no fossil or archeological evidence of goats in the Holocene. However, he reported that fossils of ancestral goats (*Oreamnos harringtoni*) at least 70,000 years old were recovered from a site at Palisades Reservoir in Idaho. This is in the southeastern quadrant of the GYE.

In an interesting interpretation of the paleontological evidence as it might be applied to modern management issues, Laundré (1990:40) suggested that because the GYE's "native floral and faunal components" are suitable for goats, "goats could also not be considered [an] ecological exotic." To our knowledge, this is the only time the concept of "ecological exotic" has been introduced into the published scientific dialogue relative to mountain goats in YNP. The concept has not fared well, or had noticeable effects on today's dialogues over mountain goats in YNP, perhaps because National Park Service (NPS) management policies do not endorse such a generous definition of native. However hospitable the ecosystem might be to introduced goats, a continuous 70,000-year gap in the known record of goat presence is too large to ignore. Though it could likewise be argued that Yellowstone Lake's native components are suitable for lake trout (*Salvelinus namaycush*), no one seems to be mistaking the clandestinely introduced lake trout that now threatens native fish in the lake for some type of "ecological native" (Varley and Schullery 1998).

Houston and Schreiner (1995) describe a parallel situation in Grand Canyon National Park, in which some paleontologists objected to the removal of burros (*Equus asinus*) from that park by NPS managers who regarded them as nonnative. The paleontologists argued that burros were "the ecological equivalents of late Pleistocene equids" that had become extinct in the area about 11,500 years B.P. In this instance the ensuing court case supported the NPS managers' interpretation that the ecological equivalent argument was not in keeping with NPS policy.

To reach beyond published literature, we consulted with a number of experienced GYE archeological and paleontological investigators. Their familiarity with GYE sites, through their own published and unpublished work and that of others, included no knowledge of any mountain goat fossils from the Holocene (J. Francis, E. Hadly, C. Hill, A. Johnson, J. Schoen, personal communication).

Faunal images in rock art sites in the GYE have not to our knowledge been inventoried by species for the entire ecosystem. Greer and Greer (1998) reviewed images at 50 sites in southwestern Montana. A few contained "zoomorphs," including 7 bison (*Bison bison*), 4 bears (*Ursus* spp.), 2 deer (*Odocoileus* spp.), 2 snakes, 2 mountain sheep (*Ovis canadensis*), 2 horses, and 5 "four-legged generic descriptions that cannot be identified at this time due to lack of information on the site forms" (Greer and Greer 1998:61). Again, our consultation with a number of regional authorities on rock art revealed no knowledge of any mountain goat images in GYE rock art (S. Conner, J. Francis, M. Greer, A. Johnson, M. Pavesic, J. Schoen, personal communication).

So far, therefore, the archeological and palentological evidence is entirely negative for mountain goat presence in the GYE prior to the arrival of Euro-Americans.

THE HISTORICAL RECORD

The earliest review of the historical record (i.e., written documents and recollections of early residents) of YNP for evidence of mountain goats was probably that conducted by novelist Owen Wister, who sought references to goats anywhere in the state of Wyoming (Wister 1904). Wister's report, though informal, was apparently based on considerable effort in communicating with experienced local residents and hunters. He concluded:

> There seems to be a sort of goat tradition in Wyoming, here and there. This myth is, to be sure, highly sublimated. You don't hear that

> goat used to be upon this or that definite mountain, or that So-and-So saw a man who saw a goat, or whose wife or uncle saw one; it never comes as near as that; yet still faintly in the air of the Continental Divide there hovers this vague rumor of the animal (Wister 1904:248).

A more formal search for historical evidence of mountain goats in Wyoming was made by Skinner (1926), who interviewed many knowledgeable locals and found no reports of goats anywhere in Wyoming or in YNP. Laundré (1990) reviewed a few early accounts of the GYE and reached the same conclusion.

For some years we have been searching all available documentary evidence of wildlife in the GYE prior to 1882 (Schullery and Whittlesey 1992, 1995, 1999a, 1999b, Whittlesey 1992, 1994, Schullery 1997). We are unaware of any previous investigator who has used more than about 20 early accounts of YNP to determine wildlife conditions and abundance in the early historical period (roughly 1800–1880). As mentioned above, the overwhelming majority of early accounts of YNP were concerned with other matters, especially the park's well-advertised geothermal wonders and scenery, but a surprising number of people did at least mention wildlife in their accounts. We are now well past 250 separate accounts of pre-1882 wildlife in the GYE and are preparing a book-length manuscript analyzing them.

In that considerable body of material, observations of mountain goats are practically nonexistent, and even discussions of mountain goats are very rare. Because these few discussions are of interest both historically and historiographically, we will review them in detail here.

Two early accounts by actual visitors to the region stated that mountain goats were present in the GYE. Both are instructive examples of the difficulties of using these early accounts. In September 1864 a prospector named Robert Vaughn and companions traveled from the gold diggings at Alder Gulch, Montana, near present-day Virginia City, to newly discovered gold-bearing areas at Emigrant, Montana, on the Yellowstone River north of present YNP (Fig. 1). Vaughn's account of their trip is brief and vague as to their travel route. He said they crossed "the headwaters of the Madison, Jefferson, and Gallatin rivers" (Vaughn 1900:35). The true headwaters of the Madison and Gallatin rivers are in YNP, but it seems to us highly improbable that the party would detour 50 or more miles south of their intended goal (Emigrant is about 60 miles due east of Alder Gulch) to reach the true headwaters of these streams. We suspect that they simply traveled east and crossed those streams well above their best-known reaches but also well below their true headwaters. We recognize that this is conjecture on our part, but it seems unlikely that these men would have detoured so far out of their way, or that they could have done so and still reached the Emigrant area in the time they did. Due to the rough country (e.g., "we were delayed several times by the dense pines that grew so thick in some places that we had to chop our way through" [Vaughn 1900:35]), it took them 7 days to reach the Yellowstone River somewhere "many miles" upstream from Emigrant. This would suggest that they reached the Yellowstone River not far north of present YNP (the north boundary of present YNP is roughly 30 river miles south of Emigrant).

Vaughn mentioned that on their way to Emigrant, in unspecified mountains, they discovered "a great quantity of petrified wood" in a small valley (Vaughn 1900:35). Petrified wood exists in the Specimen Creek drainage of northwestern YNP and is common in drainages farther north in the Gallatin National Forest as well. We assume that the petrified wood was found in one of these drainages. It was also in these mountains, apparently, that they made their mountain goat sighting:

> The mountains were very steep. On a cliff about one hundred yards off stood a Rocky mountain goat. At first we thought it a domestic sheep, for it was very white, bleated, and acted as if it was glad to see us. But then, as there were no settlers within several hundred miles, we could not imagine how a sheep could get to such a place. While we were discussing the matter, the animal leaped over cliffs and up the mountain as if it was on level ground, and this satisfied us all that it was a Rocky mountain goat. Not one of us had seen one previously (Vaughn 1900:35).

This is the only firsthand report of an observed mountain goat in the GYE that we have yet located from the period before 1882. For several reasons, it is problematic as evidence. These observers had never before seen a mountain goat. We do not know if Vaughn was able to distinguish a goat from a bighorn sheep. For all we know, he was like many first-time visitors to present-day YNP and other western mountain parks, who, in our long experience with such people, refer to bighorn sheep as goats. Some of these people are simply unaware that there are two animals, or that the distinction between them might be significant to other people. Others confuse the names, the way many regional residents today refer to local ground squirrels (*Spermophilus armatus*) as "gophers" (*Thomomys talpoides* is the local pocket gopher, but most people are probably unaware of what gophers look like specifically, and just assume that small burrowing animals can fairly be called gophers).

There are also questions about the description of the animal itself. Bighorn sheep are often quite pale and, again in our experience, are sometimes described as white by YNP visitors. Bighorn sheep ewes have small horns about the same size as goat horns. Sheep are quite agile on cliffs. Again, based on our own experiences, we know that some park visitors see sheep in conditions like these and call them goats (on the other hand, it is likewise possible that some early traveler who did see goats might have called them sheep).

Yet, though the account is speculative, it cannot absolutely be proven in error. We must consider the known proclivity of the occasional mountain goat to make a long-distance foray, such as is occasionally witnessed in YNP today. Apparently, it is not impossible that a goat from the native population farther west was just then traveling in this region, just as it is possible that this was not only a goat but a member of some resident band of goats that Vaughn and his companions did not see. After all, it is an interesting coincidence that of all the locations in the GYE in which such a sighting could have been reported, this one occurred reasonably close to the western edge of the ecosystem, that being the edge closest to known native mountain goat habitat farther west.

Our conclusion is that this report must be treated as modern park naturalists would treat a similar report. Based on the low level of knowledge of the observers and the vagueness of the description (Were the horns light or dark? Was the hair long or short? Did the body have the angularity of a goat's?), such a sighting would be regarded as intriguing but unreliable. In many years of dealing with the public in YNP, we have both dealt with great numbers of visitors as they reported wildlife sightings; neither of us would regard this as a trustworthy mountain goat sighting and would consider it more likely to have been a sighting of a bighorn sheep ewe or young ram.

The second report is not an actual observation but a statement of mountain goat presence. Photographer Henry Bird Calfee and his companion Macon Josey visited the park area in 1871 and left several mentions of wildlife there. Calfee stated that while the two were camped near Mud Volcano (Fig. 1), and nearly out of provisions, there was no cause for concern:

> Meat however was in abundance. It consisted of buffalo, moose, elk, bear, wolverine, black and white tail deer, antelope, mountain sheep, goat or ibex, wolf, lion, fox, coyote, badger, otter, beaver, mink, marten, sable, rabbit, muskrat, porcupine, rock dog, squirrel, chipmunk, grouse, goose, duck, swan, pelican, crane, brant, eagle, owl, hawk, crow, raven, blackbird, blue-jay, snow bird, curlew, sage hen, prairie chicken, and wormy trout, with which the upper Yellowstone and Lake abounded. This bill seems elaborate, but all could be gotten within five miles of our camp and in a very short time (Calfee 1896:2).

This is a singular list, not only because it seems to suggest that Calfee was willing to eat quite a few things most modern travelers would not consider appetizing, but also because he mentioned both sheep and goat. Calfee would make later visits to the park area, but this was probably his first. He is to some extent a known personage, with a documented local history that gives us no particular reason to discount his observations outright.

Nevertheless, his statement's worth as evidence is compromised in at least 3 ways.

First, there is no suitable mountain goat habitat within 5 miles of Mud Volcano (nor is there suitable sheep habitat). This is a key point because if Calfee had not placed that limitation on his statement, and were it not compromised in the other ways listed below, he potentially would be a considerably more credible witness than Vaughn.

Second, the sequence of the naming is confusing. When he wrote "mountain sheep, goat or ibex," was he in fact giving 3 alternative names for the same animal (as a writer today might say "the wolverine, glutton or carcajou")? Or was the mountain sheep meant to be one animal, and the "goat or ibex" meant to be another?

If the latter, then we have our 3rd compromise of the evidence, because if he regarded "goat" and "ibex" as interchangeable terms, it seems likely that he was thinking of a sheep-like animal rather than a mountain goat–like animal. Ibex (*Capra ibex* and others) are Eurasian and African animals with relatively long, curved horns; in both coat and general conformation they much more nearly resemble North American bighorn sheep than North American mountain goats (Nowak 1991).

This reasoning on our part necessarily assumes that Calfee was in fact knowledgeable enough to know what an ibex looked like. It is our suspicion, in any case, that Calfee was merely listing any and all even marginally edible species of Rocky Mountain wildlife he could think of at the time, rather than intending for readers to draw a 5-mile-radius circle around Mud Volcano and seriously expect to find inside it everything he mentioned.

A 3rd statement from the period (though just after 1882) also suggested by implication that mountain goats were present. In the announcement of the prohibition of public hunting in YNP, issued on 15 January 1883, Acting Secretary of the Interior H.M. Teller said this:

> The regulations heretofore issued by the Secretary of the Interior in regard to killing game in the Yellowstone National Park are amended so as to prohibit absolutely the killing, wounding or capturing at any time, of any buffalo, bison, moose, elk, black-tailed or white-tailed deer, mountain sheep, Rocky mountain goat, antelope, beaver, otter, martin, fisher, grouse, prairie chicken, pheasant, fool-hen, partridge, quail, wild goose, duck, robin, meadow-lark, thrush, goldfinch, flicker or yellow hammer, blackbird, oriole, jay, snowbird, or any of the small birds commonly known as singing-birds (Teller 1883).

Like Calfee's list quoted above, this list reveals a curious mixture of ignorance and knowledge of the native fauna of YNP. Some listed species did not occur in the park, and at least one other is listed twice (bison and buffalo). It has been suggested that this list was most likely compiled in Washington, perhaps by a clerk with limited knowledge of the park (Schullery 1997). The text of the letter, including the mention of mountain goats, reappeared in later documents relating to park management, such as Senator George Graham Vest's unsuccessful 1885 bill to strengthen law enforcement in the park (e.g., Forest and Stream 1885).

It must be kept in mind that most observers of that period, including almost all park administrators, had no formal scientific training and little awareness of taxonomy (in 1880, Superintendent Philetus Norris stated that there were 6 kinds of bears in Yellowstone). In any case, no park administrator from this period suggested that mountain goats actually did reside in the park.

On the other hand, Superintendent Norris specifically stated that he was unaware of any goats in the park. In his annual report for 1880, Norris said that

> although the web-footed, snow-loving white sheep, or Rocky Mountain goats are numerous in many of the adjacent snowy regions, I have never seen one within the Park, but the true big-horn sheep are abundant on all the mountain crests, as well as on their craggy spurs and foot-hills throughout the Park, which they never leave (Norris 1881:40).

Here again we see the interchangeability of names: to Norris, the mountain goat was also the "white sheep." Also, Norris suggested that goats inhabited "snowy regions" adjacent to the park. Whether by this he meant neighboring mountain ranges or had in mind some farther-reaching sense of the word *region*, we cannot tell. Writing in the somewhat florid prose of the day, Norris tended sometimes to speak in sweeping terms, so we are hesitant to interpret "adjacent snowy regions" to mean lands immediately adjoining the park.

The only other specific mentions of mountain goats prior to 1882 were statements of their absence in large portions of the GYE. Charles Blackburn spent nearly 2 years prospecting "in the country lying about the headwaters of the Yellowstone and the other great rivers that have their sources in the Wind River Mountains" (Blackburn 1879). The dates are uncertain, but he probably began in the region in 1877, and his article was published in July 1879. In a section entitled "Zoology," he described the wildlife:

> Elk and mountain sheep are very plentiful through all the ranges of the Yellowstone

> country, being generally found near the snow in the summer, where the grass is new and tender. The mountain goat (*Aplocerus montanus*) was not observed in any of the ranges, but has been reported by Indians to exist in the mountains farther north (Blackburn 1879:2904).

Blackburn evidently understood that there is a distinction between sheep and goats (we are assuming he could likewise distinguish them in the field). Beyond that we know nothing of his qualifications as an observer of wildlife. His delineation of the country he had in mind is imprecise, but probably included the YNP area, and perhaps even the entire northern half of the GYE. Native mountain goat populations "farther north" apparently would be those populations associated with the Northern Continental Divide Ecosystem (Chadwick 1983), which is slightly west of north of the GYE.

Our last mention of goats also covered a wide and not clearly defined region. In an extended account of a trip through YNP in 1884, the naturalist-anthropologist George Bird Grinnell reported on the opinion of a local hunting guide, one of the Rea brothers. The Reas ran a stage station near the Henry's Fork, in eastern Idaho, not far west of YNP. The brother that Grinnell questioned had "been in the country seventeen years and may therefore be supposed to know it fairly well."

> He stated in a conversation I had with him that game is still quite plenty here. There are a few moose; elk and deer are rather abundant, as are also bears, the black and cinnamon being common, while the grizzly is not often seen. Mountain sheep are very scarce. In reply to specific inquiries as to white goats and caribou, he stated that he had never known of either being found in the neighborhood or in the vicinity of the Park. The nearest points where goats are to be found is, he said, between Bitterroot and the Bighole, a long distance to the westward (Grinnell 1885:3).

Rea was an experienced local observer, but it is our impression based on our reading of this region's history that he was something of a self-promoter. He had some credentials as a wildlife expert. In 1874 he was apparently collecting specimens for "Prof. Ward's Natural Science Academy" in Rochester, New York (this is the same Ward who would later become well known for his scientific instrument company). On the other hand, in 1875 he had been sentenced to 15 years in the territorial prison for his part in the wrongful death of another man (Bozeman Avant Courier 1874, 1875a, 1875b). This is not a feature of his biography that tends to strengthen confidence in his credibility (he evidently did not serve the full sentence because he was free to talk with Grinnell in 1883). Like many other early information sources, his reliability is not completely understood. Such are the vicissitudes of these anecdotal historical sources, but we know of no reason why Rea would intentionally misstate his impression of mountain goat absence from the region. If we assume that native mountain goat range was at that time similar to what we believe it is today, then it appears that Rea agreed with modern mountain goat authorities, as cited above, on the range of the species.

YELLOWSTONE NATIONAL PARK IN EARLY WILDLIFE MANAGEMENT

YNP was established by act of Congress in 1872, with very little institutional direction provided. Early managers were left largely on their own to develop policies (Haines 1977, Schullery 1997, Pritchard 1999). Some of the most important values we associate with national parks today were barely embryonic in American society at that time, and wildlife management policy in YNP could hardly be said to exist outside minimum standards common on other public lands. Public hunting was permitted in YNP until 1883 (see discussion of Teller letter, above). In that year political pressure, primarily from sportsmen, resulted in hunting being outlawed. Abruptly the park became a wildlife reserve of great size and unrealized opportunity.

But most details of management policy were still unresolved, or would undergo scrutiny and reconsideration. It was simply assumed, for example, that the landscape and its wildlife could be "improved" by the introduction of nonnative species. Several species of sport fish were successfully introduced; native fish species suffered tremendous declines and even disappearances in many drainages during this process (Varley and Schullery 1998).

Less well known now are numerous proposals to introduce a remarkable variety of nonnative birds and mammals to the park, including mountain goats. In 1902, Acting Superintendent John Pitcher pointed out that "the scarcity of birds [in YNP] has frequently been noted, and it has been suggested that the capercailzie and blackcock, game birds of northern Europe, might be introduced in the Park" (Pitcher 1902:7; he was apparently referring to Capercaillie, *Tetrao urogallus*, and Black Grouse, *Tetrao tetrix*). Captain Pitcher was enthusiastic about these proposals and pointed out that a further advantage of bringing in these birds would be that "they would spread into the neighboring country and soon afford fine bird shooting where there is little or none at present" (Pitcher 1902:7). In 1903 as distinguished a conservationist and naturalist as President Theodore Roosevelt wrote enthusiastically about "naturalizing" some species of pheasant and other game birds to YNP. He was also eager to bring chamois (*Rupicapra* sp.) in, "which certainly ought to do well there" (Roosevelt 1951:470–471). In 1907, Superintendent Samuel Baldwin Marks Young pointed out that "with intelligent management and comparatively little expense a greater variety of birds and mammals could be successfully added and propagated within the park" (Young 1907a).

Superintendent Young may have come closer than any other early manager to realizing the dream of an artificially enriched ungulate ecosystem in Yellowstone. In April 1907, in the final months of Major Pitcher's acting superintendency, the secretary of the interior authorized the expenditure of $300 "in relation to the procuring of white goats and domesticating the same in the Yellowstone National Park" (Garfield 1907). When Young replaced Pitcher in June 1907 (Haines 1977), he quickly pursued this project, corresponding with a variety of possible sources of goats in Montana and British Columbia. His plan included what would today be termed a "soft release," in which the goats would be held in a pen for some time prior to release (Young 1907b). Dan Doody, of Nyack, Montana, on the southwest boundary of what would become Glacier National Park (GNP) a few years later, was selected to capture the goats, but had difficulty keeping them alive long enough to transport them (Doody 1907). Though Young continued to correspond with one other possible source of mountain goats in 1908, it appeared that the project just fizzled. We find no record of goats purchased or goats shipped to YNP, or of goats released in YNP. We have not been able to determine why or when this idea was abandoned, though it could be that when Young left YNP late in 1908 he took with him all existing administrative enthusiasm for the project.

The dream of introducing mountain goats to YNP died slowly. As late as 1915, the Game Preservation Committee of the Boone and Crockett Club recommended that goats be introduced into YNP (Trefethen 1961). The general mood of these and other recommendations was that more was better—that nature could be enriched, indeed improved upon, by the judicious actions of humans. The wild setting was not seen as an ecological whole with some innate integrity; it was seen as the raw material for making the most of a good thing by adding more good things.

Such manipulations of natural settings and nonnative species were simply routine in North America at the time; they were undertaken widely—and often failed—but have been a staple of professional wildlife management since the late 1800s. But opposing views were surfacing as well in the early 1900s. In their important article, "Animal Life as an Asset of National Parks," published in *Science* in 1916, professional biologists Joseph Grinnell and Tracy Storer said that just as dogs (*Canis familiaris*) and cats (*Felis catus*) must be kept from roaming free in national parks,

> equal vigilance should be used to exclude all non-native species from the parks, even though they be non-predaceous. In the finely adjusted balance already established between the native animal life and the food supply, there is no room for the interpolation of an additional species (Grinnell and Storer 1916: 379).

Without specifically saying why, beyond the assertion that it would upset a "balance," these naturalists firmly opposed any additions to park fauna.

These sentiments were soon echoed and broadened by the scientific profession. By the 1920s, as the community of wildlife scientists and management professionals matured and grew, a number of societies, such as the

Ecological Society of America and the American Association for the Advancement of Science (AAAS), spoke out against adding more nonnative species to national parks. In 1921 the AAAS clarified its opposition to introducing nonnative species: national parks were "rich fields for the natural sciences . . ." where the native flora and fauna were "more nearly undisturbed than anywhere else" (Wright 1992:37). In the 1870s, YNP had been recognized by its first scientific explorers as a kind of laboratory; the AAAS resolution of 1921 suggested that the park's value was now increasing because its wilderness setting and undisturbed biotic community were becoming increasingly rare elsewhere. YNP was being perceived more broadly as a living museum of primitive conditions, and the value of such an institution was likewise being more broadly appreciated (Pritchard 1999).

AN EMERGING NPS AND YNP POLICY AGAINST NONNATIVES

Starting after 1900, YNP seemed to develop a policy on nonnative species in rather haphazard fashion, on a case-by-case basis. The earliest official rejection of a nonnative species probably occurred in the area of fisheries management:

> In 1907 a U.S. Fish Commission employee, D.C. Booth, was given a reprimand by his superior for planting rainbow trout in Yellowstone Lake. This is the earliest instance of which we are aware of Yellowstone fisheries managers overtly seeking to protect native strains of fish from dilution. And in 1908, when no less a heavyweight than the U.S. Commissioner of Fisheries proposed that smelt be stocked in Shoshone and Yellowstone Lakes, it couldn't have been easy to say no—but the park's military managers did (Varley and Schullery 1998:97).

For many years after 1908, nonnative species of fish that were already in the park at that date were still managed and fostered as part of the park's very popular sport fishery. All that happened in 1908 was that the addition of new species was officially disallowed. But that was an impressive development considering that at this same time Superintendent Young was shopping for mountain goats.

The sentiment of opposition to nonnatives in parks was translated into formal policy in 1936, based on the 1933 publication of what is now known as Fauna No. 1, an influential report on park animals by George Wright, Joseph Dixon, and Ben Thompson. The report, which reviewed nonnative animal problems in several parks, emphasized in all its proposed regulations the protection of and preference for native species. Native species that had been extirpated were to be brought back (if the species in question had become generally extinct and no source could be found, it was not to be replaced with some "related form" of animal). Nonnative species already established in parks were to be eliminated. If elimination was not possible, their numbers were to be "held to a minimum" (Wright et al. 1933). In a passage that might be especially relevant to the current YNP mountain goat situation, Wright and his colleagues warned that it was not enough to wait until nonnative species were established:

> That the threatening invasion of the parks by other exotics shall be anticipated; and to this end, since it is more than a local problem, encouragement shall be given for national and State cooperation in the creation of a board which will regulate the transplanting of all wild species (Wright et al. 1933:148).

Since 1936, then, nonnative animals have been officially and decisively regarded as unwelcome in YNP. Since that time, through a series of revisions and modifications of policy statements, the agency's position on nonnative animals has been reaffirmed. All stocking of park waters (with native or nonnative fishes) ceased about 40 years ago (Varley and Schullery 1998). The language of policies on nonnatives has evolved to reflect changing understanding of ecological communities, but the statements against exotics have remained. For example, in the 1970 version of Administrative Policies for the National Parks and National Monuments of Scientific Significance (Natural Area Category), the policy was about as unequivocal as was practically possible: "Nonnative species of plants and animals will be eliminated where it is possible to do so by approved methods which will preserve wilderness qualities" (NPS 1970:56).

In 1988, after additional revisions, the policy seemed rather less absolute. On the one hand, the definition of an exotic species was still reasonably concise:

> Exotic species are those that occur in a given place as a result of direct or indirect, deliberate or accidental actions by humans (not including deliberate reintroductions). For example, the construction of a fish ladder at a waterfall might enable one or more species to cross that natural barrier to dispersal. An exotic species might also be introduced through seeds in the droppings of an animal that has fed on an exotic species outside the park. The exotic species introduced because of such human action would not have evolved with the species native to the place in question and, therefore, would not be a natural component of the ecological system characteristic of that place (NPS 1988a:4.11).

On the other hand, the agency's responsibility toward exotic species was not as absolute as it had been in earlier policy expressions. Instead, agency obligation to control exotics operated on the basis of a continuum of risk. According to NPS-77, the Natural Resources Management Guideline that complemented and interpreted the policy for managers, exotic species most likely to cause harm to the ecological system were to be fought most aggressively, and those that were relatively benign could apparently be ignored:

> Control or eradication will be undertaken, where feasible, if exotic species threaten to alter natural ecosystems; [or] seriously restrict, prey on, or compete with native populations (NPS 1988b:289).

It appears that this guideline would allow ecological specialists to determine if mountain goats that have colonized YNP in recent years have exhibited any of these listed effects, and are thus in grave enough violation of policy. The policy does not quantify what constitutes a sufficiently harmful alteration of a natural ecosystem, or what exactly is meant by serious restriction, predation, or competition.

A spectrum of interpretations of this policy is possible, and such interpretations are informally offered by people engaged in conversations over mountain goats invading YNP. On one end of the spectrum are those who take what might be called the philosophical high road and regard any nonnative presence as necessarily a violation of the NPS mandate and the ecosystem's fundamental purity. On the other end of the spectrum are those who selectively welcome some nonnative species, whether because the species serves to fill a role vacated by an extinct native or because the species is merely appealing for aesthetic reasons. It is both interesting and a little puzzling that neither the policy nor NPS-77 seems to reflect aesthetic concerns, such as the possibility of a visitor experience being compromised by viewing nonnative species in a national park, as significant factors in deciding whether or not to remove such animals.

AN INTRIGUING DEVELOPMENT IN RECENT HISTORY

The more recent history of mountain goats in the GYE provides a fascinating example of the complexities of policy interpretation. In the past half century, mountain goats have been established by state game managers of Idaho and Montana in hospitable habitats to the north, northwest, west, and southwest of YNP (Peck 1972, T. Lemke and N. Varley personal communication). Goats from populations introduced into Montana north of the park are already established in northeastern and northwestern YNP. However, it is regarded as conceivable that *native* goats currently residing farther west of the GYE could also make their way into the park by following the crest of the Centennial Mountain Range east to the Gallatin Mountain Range in northwestern YNP (Laundré 1990, Wilkinson 1990; Fig. 1).

A decade ago the very suggestion of the possibility of such a situation attracted the attention of the media, as well as then-prominent animal-rights advocate Cleveland Amory (Wilkinson 1990). The media report posed an interesting dilemma facing managers. By policy, YNP managers should resist or at least disapprove of the northern invasion because these goats were from introduced populations. But if native mountain goats moving in from the west were part of a non-human–caused colonization, policy direction seems to be that the animals would simply be accepted as a new native species. National park ecosystems, like all others, have hosted invasions of new species for thousands of years; such changes occurred ever since the ice retreated more than 10,000 years ago, long before Euro-Americans arrived to influence the setting. By implication, at least, the current policy (quoted above) seems to accommodate late arrivals: species colonizing parks today unaided are apparently welcome.

In discussing the possibility of dual mountain goat colonizations from both native and nonnative populations, former YNP Superintendent Robert Barbee, a pragmatic and realistic manager, said that to fight off the species on one boundary and welcome it along another did not "pass the red-face test" of real-world management. No matter how closely such an approach might adhere to policy, it would look idiotic to the public (R. Barbee personal communication). Whether it would actually *be* idiotic is another question, but it seems safe to say that few NPS managers would disagree with Barbee's prediction of a negative public reaction.

The issue is not without opportunities for scientific inquiry. First, could it be established which population the invaders were from? Or, are the native goats west of the GYE and the introduced goats in Montana too closely related for distinctions to be genetically meaningful (if *meaningful* can even be defined in this context)?

Then, if goats from a native population did migrate to the park, was their migration facilitated by humans? For example, could predator control either in the home range of these animals or along the migration route have made travel easier for them than it would have been 200 years ago? For another example, it appears that between about 1830 and 1880, bighorn sheep numbers declined dramatically in some parts of the GYE, perhaps in part because of introduced livestock diseases (Schullery and Whittlesey 1992); did this emptying of habitats have any effect on the hospitality of the GYE to colonizing mountain goats since then? Last, the native range of the mountain goat has changed dramatically with the retreating ice of the last ice age and should not be regarded as having achieved some stable state (Chadwick 1983). Ongoing mountain goat distribution changes independent of human activities may have been underway at the time of Euro-American arrival in the GYE, and these could also affect the "nativeness" of goats. It may be necessary to address questions like these to fully consider how "natural" a mountain goat colonization of the GYE would be, even if it were effected by goats from native populations.

One somewhat caustic reader of an earlier version of this manuscript said that the previous paragraph's questions amounted to "milking mice," that is, dealing with trivially obscure issues. We disagree. If the mountain goat invasion of YNP ever became a controversial enough issue to result in a court case, we believe the judge would require the milking of these very mice, and probably quite a few others. Nativeness is the central issue in this situation, and the court would certainly recognize that science can be applied to clarify the origin of the goats in question (it seems likely to us, for example, that if these questions ever did have to be answered in court, DNA analysis would probably be called for, in an attempt to distinguish goats from different regions).

But the current status and source of YNP mountain goats is reasonably clear. T. Lemke (personal communication) reported that the only persistent concentrations of mountain goats in YNP occur in the northeast and northwest corners of the park, with occasional appearances by wanderers in other park locations. According to Lemke, these colonies are extensions of known introduced populations in the Gallatin and Absaroka Mountain ranges to the north of the park. As of 1999, then, YNP is known to have been colonized only by goats from introduced populations in Montana. The suggestion that some or any mountain goats could enter the park from native populations moving from the west appears to be just that: a suggestion.

On the other hand, there is some uncertainty about how close native goats have approached the GYE. In 1990 the Bureau of Land Management (BLM), Dillon Resource Area, prepared a draft environmental assessment (EA) to "reintroduce mountain goats in the Sheep Mountain area adjacent to Red Rock Lakes National Wildlife Refuge" (Lewis 1990; Fig. 1). Sheep Mountain is well within current definitions of the GYE (Glick et al. 1991). The EA stated that "mountain goats are considered as being historic residents of this area" (Roscoe 1990) but provided no documentation on this point. The author of the EA recently explained to us that the introduction process stopped when the BLM was unable to find evidence that goats were native; introducing a nonnative species in these circumstances would have been against BLM regulations. "So at that point the project stopped" (J. Roscoe personal communication).

In this situation the BLM was in a dilemma much like that currently faced by YNP. According to the EA, goats were already close and even had been observed nearby in the Centennial Range:

> No recent observations of mountain goats have been made in the proposed release area. A single adult goat was observed on Slide Mountain on the west side of the Odell Creek drainage by refuge manager Barry Reiswig on October 25, 1983. Several observations of mountain goats were made in 1984 and 1985 near Spencer, Idaho, which is approximately 25 miles southwest of the project area (Roscoe 1990).

It was not possible at that time to know the source of the goat seen on Slide Mountain, which is about 10 miles west of the proposed introduction site (but still in the GYE). It could conceivably have been either from farther west (the direction of the native populations) or from an introduced population in the Madison Range to the northeast (J. Roscoe personal communication). It is also interesting to note that the proposed source of goats for this project was Olympic National Park (ONP).

The issue of a potential native mountain goat migration to YNP was perhaps first brought to the attention of the scientific community by Laundré (1990) and was picked up by the media about the time his report was published. In his report Laundré said:

> Given time, goats might have eventually moved back into the Yellowstone Ecosystem, as they may presently [*sic*] be doing from historic range into the Centennial Mountains. Currently, all this is speculation and the rapid expansion of goat range in the mountains north of Yellowstone Park would tend to contradict this hypothesis (Laundré 1990:40).

Notice that Laundré said only that goats "may" be migrating into the Centennial Mountains, a range west of YNP. He did not suggest that they were on their way to YNP, and he seemed uncertain if such a migration was a likelihood. As the situation in the Centennial Range described above suggests, by the time that Laundré was writing, it was already very difficult to establish the "identity" of mountain goats moving through the gap between known native goat habitat farther west and introduced mountain goat habitat in the GYE.

Meanwhile, the hypothetical dual nature of the mountain goat colonization of YNP has somehow risen from the status of an academic but very interesting "what if" question to the status of a genuine dilemma. Though all mountain goats currently in YNP are reasonably traced to the introduced Montana populations, the possibility of a migration of goats into the GYE or YNP from native populations farther west seems to have become, at least in recent dialogues, almost equal in significance to the reality of the known migrations from the north. The possible immigration of native goats has become, in the words of Wister, highly sublimated. Rather like scholarship's inability to demonstrate absolutely that there were no mountain goats in the GYE prior to 1882, scholarship's apparent inability to determine absolutely the origin of every single mountain goat that has entered or may enter YNP may be adding to the current institutional timidity over what to do next. Those concerned with the mountain goat issue seem stymied by Wister's "vague rumor of the animal."

CONCLUSION

In this paper we have reviewed all early mentions of mountain goats in the GYE that we have found. If those early accounts were read alone, removed from their full documentary context, they might give the casual reader reason to suspect that at least a few goats were present in the GYE in the mid-1800s. Indeed, we recognize that the possibility may have existed for the occasional exploration-minded goat to have entered the GYE from the west. There may even have been a possibility that a small, unnoticed population of mountain goats existed in the GYE before 1882. But the historical material we have examined so far provides no convincing evidence of either individual animals or a population existing in the GYE before 1882.

Brandborg (1955), in attempting to make the best use of early travelers' accounts of mountain goats in Idaho, has pointed out that

> the absence of references to mountain goats in early journals is not proof that they did not exist in an area. The route of the travelers along valley bottoms and through open terrain during midsummer, when the goats were at high elevations, precluded observations of them (Brandborg 1955:16).

As we have explained in some detail above, we agree that travelers who wrote about their journeys could neglect to mention wildlife they saw. In fact, we think many if not most early travelers in the GYE did just that. It is certain that virtually none of them kept conscientious records of every animal they saw. However, in the case of the GYE and many early accounts of it that we have analyzed, Brandborg's 2nd statement, about the route traveled, does not apply. Many of our observers, being trappers, prospectors, hunters, and other adventurous types, did not confine themselves either to the valley floors or to the summer season (Schullery and Whittlesey 1992). It is our opinion, based on experiences in observing goats in GNP, Mount Rainier National Park, and YNP, that, had goats been present in a region as thoroughly traveled as was the GYE in the early historical period, they would have been seen. It could be argued that with the possible exception of Dall's sheep (*Ovis dalli*), no other North American ungulate species is so perfectly designed by nature to be observed from a great distance. Not only does the mountain goat stand out brightly against the often dark background of its preferred habitat, but also it does so at sufficient elevations that it is visible from much of the surrounding lower country.

We therefore believe that Fischer's fallacy of negative proof, though a valid and essential guide in the use of historical material relating to wildlife, needs a kind of corollary. This corollary is that it is possible to accumulate such a large volume of negative evidence as to leave very little room for the affirmative alternative. The negative evidence will never absolutely establish that no animals of a given species existed in a region, but it can accumulate to a volume and depth sufficient to demonstrate beyond any reasonable doubt that such animals were scarce at best.

On the simplest level, that of reported sightings, the great wealth of firsthand observations we have examined makes it clear to us that if mountain goats did indeed exist somewhere in the GYE in the early historical period, they were extraordinarily and uncharacteristically invisible to virtually all travelers who were interested enough in wildlife to record their observations. Without a single verifiable or even reliable sighting to prove goat presence, with a few reports that state that goats were not present, and with many more sources that simply do not mention goats, we believe that managers are justified in declaring the mountain goat a nonnative species in the GYE and YNP.

National park managers must often make decisions based on incomplete information, and they must often acknowledge that complete information is not attainable. Determining the nativeness of a species may be such a situation, and the YNP mountain goat issue is not the first time it has arisen. Attempts to reduce mountain goat numbers in ONP have featured disagreements over whether the animals were truly nonnative. These disagreements focus largely on competing interpretations of surprisingly few problematic early historical sources (Lyman 1994, 1998, Houston 1995, Houston and Schreiner 1995, Hutchins 1995). Rocky Mountain National Park and Grand Teton National Park also face similar decisions concerning managing goats, as well as questions over the nativeness of the species (Gross et al. 2000). Houston and Schreiner (1995) review other variations on the native-nonnative issue in other national parks.

Even in present-day national parks, there are disagreements over the presence or absence of a species. A persistent issue in the debate over Yellowstone wolf (*Canis lupus*) recovery involved the possibility of a lingering remnant population of native wolves (U.S. Fish and Wildlife Service 1994). Debate over the reintroduction of grizzly bears to the Bitterroot Mountains on the Idaho-Montana border now features disagreements over whether grizzly bears are totally absent from the area (Devlin 1999). When the debate over such an issue achieves its finest resolution—the analysis of limited evidence for which there are conflicting interpretations and which at best indicates the presence of a few animals—it is not clear with which party the burden of proof should lie, or how such disagreements might be resolved.

It is also not clear what managers are to do even if they are confronted with incontrovertible proof of the existence of a single animal of the species in question. For practical management purposes, past experience suggests that the demonstrated presence of a single animal may not be sufficient. In the case of wolf recovery in the GYE, for example, the U.S. Fish and Wildlife Service recognized that individual wolves seemed to exist in the GYE in the early 1990s (prior to the reintroduction of new wolves), but regarded these rare animals as not constituting a "population" of animals that had any likelihood of sustaining itself over time (these animals' "quality" as evidence was also suspect because they may have been escaped pets, clandestinely released animals, or, as was established in one case, recent immigrants from other wolf populations beyond the GYE). At that point in the deliberations of the U.S. Fish and Wildlife Service, it became a matter of defining a population, which was done in terms of a certain number of successfully breeding pairs over a certain period of time (U.S. Fish and Wildlife Service 1994). It was regarded as proven that wolves inhabiting the GYE prior to the arrival of the introduced wolves in 1995 did not meet this definition.

Current NPS policy and guidelines do not provide much constructive guidance for managers facing uncertainties of this sort. There are no prescriptions for what qualities and quantities of evidence are the minimum acceptable amount to establish that a species was or is present or absent. Likewise, there are no prescriptions for establishing what numbers or population characteristics are necessary for a small number of animals to constitute a native presence *as a population.*

Thus, it appears there are no indisputable criteria by which modern YNP managers can judge the appropriateness of the present mountain goat colonization even if it were established that at least one goat did inhabit the GYE prior to the park's establishment. If it were shown that a single sighting of single mountain goat did occur—if, for example, Vaughn's 1864 sighting were somehow confirmed—how can that information be applied to the current situation? Does that single sighting justify or at least make tolerable the current goat colonization of YNP from multiple artificial introductions north of the park? Put yet another way, even if there were a reliable sighting of a single goat in the GYE in 1864, does tolerating the current goat colonization of YNP equate with assuming that the single goat was the vanguard of a much larger natural colonization on the scale of the one that is now occurring? Or, to place a broader interpretation on the policy, does the existence of a single native goat in 1864 endow managers with authorization such that they can disregard these questions and simply declare the current population of goats "native enough"?

It is also difficult to interpret policy guidelines relating to whether or not these mountain goats pose a threat to the native ecosystem and should be removed. Ecological evaluation is beyond the scope of this paper, but because the issue is social as well as scientific, we should at least mention it. N. Varley (personal communication) has reported that so far he can find no evidence of significant ecological effects of goats in YNP. But the invasion is young, and recent literature on ungulate grazing systems (e.g., McNaughton et al. 1989) suggests to us it is risky to assume that an ungulate population will not affect ecosystem processes and plant communities to some extent, and current knowledge of potential goat habitat in YNP may not be capable of measuring such effects as they happen. As important, the discussion that followed the panel session at which our paper was given made it clear that other participants in the dialogue hold to a traditional principle of "purity," by which the goats must be regarded as inappropriate simply because they are nonnative, regardless of any measured ecological effects they may have. Following this line of reasoning, even if mountain goats are ecologically benign, they are inappropriate. That is to say that aside from any ecological problems they pose, they compromise the experience the park is supposed to provide.

The social issue may be the more important one in the future of goat management in YNP. It is our opinion, based on the experience of managers in ONP and on our own observations of visitors enjoying mountain goats in YNP and GNP, that people who espouse the principle of ecological purity as a justification for removing mountain goats from YNP will not stand a chance against a pro-goat constituency for whom the animal's romantic image and beauty make it an exciting addition to their recreational experience. These recreationists have a demonstrated, even willful, lack of interest in any effects that the mountain goat's presence may have on those who come to YNP to experience native wild nature. If the state of Montana (which is, after all, the source of the "problem" because it introduced the goats into nonnative ranges north of the park and has not attempted to halt their spread) and the NPS choose to continue to accommodate the colonization of the park by mountain goats, the constituency of goat enthusiasts will grow at least as fast as the goat population does and will no doubt be as strong willed and outspoken as it has been in ONP.

Management of YNP natural resources has evolved greatly since the park's creation. Such evolution has most often occurred as a matter of necessity, when an issue became politically or even ecologically pressing enough to require reconsideration. The invasion of Yellowstone Lake by nonnative lake trout, mentioned above, is an example of an issue that was immediately pressing, both because of its threat to native elements of the ecosystem and because of its potential impacts on regional recreational economics. The goats currently occupying the GYE and YNP have for some years threatened to become pressing enough as an issue, but only time will tell if they force an advancement in the complex wildlife policies of this region. Our reading of past Yellowstone history suggests that as long as no compelling ecological issue surfaces, the mountain goat colonization of YNP will probably never achieve adequate significance in the eyes of managers or other concerned constituencies to force the decision-making process into action. That is to say that so long as the goats seem benign, management reaction to them will likewise be benign, and colonization will proceed as the goats and their new environment allow.

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BIOLOGICAL INVASIONS—HOW ARE THEY AFFECTING US, AND WHAT CAN WE DO ABOUT THEM?

Daniel Simberloff[1]

ABSTRACT.—Nonindigenous species affect native ecosystems, communities, and populations in myriad ways, from plants (and a few animals) that overgrow entire communities, to plants and animals that hybridize individual native species to a sort of genetic extinction. Further, nonindigenous species sometimes interact to worsen each other's impact. These impacts are commonly seen in national parks throughout the United States. The key policy change required to alleviate this threat is a shift from blacklists of prohibited species and a presumption of harmlessness to combinations of white and blacklists and a presumption that any species may be damaging. This new guiding philosophy must be inculcated at international and national levels, which will not be easy during a period when free trade is seen as an unmitigated blessing. Within the United States, enhanced cooperation and coordination will be required among all parties (i.e., federal, state, and local agencies as well as private entities) charged with managing invasions. Internationally, the key forum is the World Trade Organization. Various management tools available to combat nonindigenous species have produced some striking successes, but new research could improve their effectiveness and reliability. There is a particular need for research on ecosystem management to control introduced species. In the face of the increasingly publicized onslaught of invaders, there is a widespread tendency to view increased biotic homogenization as inevitable. However, advances in both policy and technology could greatly slow this process and perhaps (in concert with restoration measures) even reverse it. The necessary pressure and resources to effect these changes must come from an increasingly alarmed and vocal public.

Key words: biological control, blacklist, ecosystem management, eradication, Executive Order 13112, introduced species, invasion, nonindigenous species, white list, World Trade Organization.

Biological invasions are now the 2nd leading cause (after habitat destruction) of species endangerment and extinction in the United States and worldwide. In the United States, for example, about 42% of all species listed under the Endangered Species Act are threatened in part or wholly by nonindigenous species (Wilcove et al. 1998). However, most introduced species are not invasive. Although no one can yet say what fraction of introduced species become problematic in any region, it is surely no more than a few percent; the great majority of introduced species probably do not even survive, and, of those that do, only a few invade natural ecosystems (Williamson 1996). But these few can have enormous impacts.

In addition to causing massive ecological problems, nonindigenous species impose huge economic costs not only on nature but on agriculture, silviculture, industry, and public health; and this is the real reason for the sudden surge of new activities to try to deal with them. After all, Charles Elton (1958) pointed out most of the ecological problems caused by invasions in his book, *The Ecology of Invasions by Animals and Plants,* but he did not discuss the costs, and not many people cared, not even ecologists. Recently, a preliminary report (Pimentel et al. 2000) estimates the cost of nonindigenous species in the United States alone to be over $130 billion annually, and finally everyone is eager to do something about them.

First, I will outline the kinds of problems associated with introduced species. Then I will discuss why this crisis is occurring. Finally, I will recommend means of dealing with invasive introduced species.

KINDS OF IMPACTS

All major impacts of introduced species can be exemplified by problems found in United States national parks, although some are more dramatic in other settings. The most significant problems, in terms of ecological damage, are usually caused by plant species that overgrow entire communities, replacing native, dominant plants and often most species of

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plants and animals associated with them. For example, the Australian paperbark tree (*Melaleuca quinquenervia*), Brazilian pepper (*Schinus terebinthifolius*), and Australian pines (*Casuarina* spp.) together cover approximately 650,000 ha in south Florida (Schmitz et al. 1997), including many thousands of hectares in Everglades National Park (Doren and Jones 1997).

Overgrowth and replacement of the original community is not restricted to terrestrial systems. Water hyacinth (*Eichhornia crassipes*) in Lake Victoria (McKinley 1996) and many other freshwater sites, as well as the tropical alga *Caulerpa taxifolia*, which has invaded 9 of 10 marine reserves of the northwest Mediterranean Sea (Meinesz 1999), have had similar impacts on aquatic systems. The latter species has just been found in a lagoon near San Diego (Anonymous 2000). Occasionally, an animal species can overgrow an area with devastating effects on the entire native community, as has zebra mussel (*Dreissena polymorpha*), which has invaded many freshwater systems in North America (Johnson and Padilla 1996).

Of course, an introduced species that removes a dominant plant species can have enormous impacts on the entire native community. The Asian chestnut blight fungus (*Cryphonectria parasitica*) arrived in New York on nursery stock in the late 19th century, spread over 100 million ha of the eastern United States in less than 50 years, and killed almost all mature chestnuts (*Castanea dentata;* von Broembsen 1989). Because chestnut had been a dominant tree (comprising more than one-quarter of all canopy trees in many places, including parts of Great Smoky Mountains National Park), the impacts on the native community must have been enormous. There are occasional claims that the chestnut blight invasion shows how a dominant species can be replaced with little real impact on the ecosystem (e.g., Williamson 1996). Such statements rest on ignorance; few data exist from before this invasion that allow one to assess its full impact. Where evidence exists, it suggests major changes. For example, several lepidopterans that were host-specific to chestnut became extinct (Opler 1979).

Chestnut blight is just one of many invasions that have successively removed dominant plant species from Great Smoky Mountains National Park. The European balsam woolly adelgid (*Adelges piceae*) has more recently destroyed nearly all Fraser fir trees (*Abies fraseri*), a formerly dominant species in upper elevations of the park (Campbell and Schlarbaum 1994). Additionally, dogwood anthracnose (*Discula destructiva*) is eliminating dogwoods (*Cornus florida;* Campbell and Schlarbaum 1994), while beech scale (*Cryptococcus fagisuga;* also from Europe) is spreading beechbark disease, a European fungus (*Nectria coccinea faginata*) that arrived in Nova Scotia in 1890, reached the park by 1993, and is now ravaging beeches (*Fagus grandifolia;* Simmons 1999a). The Asian hemlock woolly adelgid (*Adelges tsugae*), a huge threat to forests dominated by hemlock (*Tsuga canadensis*) in the Northeast, is nearing the park after infesting 80% of hemlocks in Shenandoah National Park (Simmons 1999b).

In addition to ecosystemic effects, many introduced species affect particular native species or groups of them. Introduced species can eat natives, for example. The brown tree snake (*Boiga irregularis*) has eliminated virtually all forest birds of Guam after invading from the Admiralty Islands (Rodda et al. 1992), while the Nile perch (*Lates niloticus*) has extinguished over 100 species of native cichlid fishes in Lake Victoria (Goldschmidt 1996). Introduced herbivores can also eat natives to extinction: goats brought to St. Helena in 1513 quickly eliminated about half the native plant species, all of which were endemic (Groombridge 1992). Pathogens can heavily impact particular native species. The introduction of Asian songbirds to the Hawaiian Islands brought avian pox and avian malaria, facilitating the decline of native forest bird species (van Riper et al. 1986). Introduced species can also compete for resources with native species. For example, in Great Britain the North American gray squirrel (*Sciurus carolinensis*) is replacing the native red squirrel (*S. vulgaris*) by foraging more efficiently (Williamson 1996). Introduced species can directly affect native ones by attacking them, rather than indirectly by depleting their resources. This is how the South American red imported fire ant (*Solenopsis invicta*), which has spread throughout the southeastern United States and has now reached California, is replacing several native ant species (Tschinkel 1993). Allelopathy is a plant analog of aggression. Thus, for example, the African crystalline ice plant (*Mesembryanthemum crystallinum*) accumulates salt, which remains in the soil when the plant decomposes and thereby eliminates native plants (Vivrette and Muller 1977). Nonindigenous species also threaten the existence of native species, at least as distinct genetic entities, by mating with them. For example, both the New Zealand Gray Duck (*Anas superciliosa superciliosa*) and the Hawaiian Duck (*A. wyvilliana*) are threatened by hybridization and introgression with the introduced North American Mallard (*A. platyrhynchos;* references in Rhymer and Simberloff [1996]). Even when there is little or no gene flow, a species can be imperiled simply by loss of productive mating opportunities. The introduced brook trout (*Salvelinus fontinalis*) threatens native bull trout (*S. confluentus*) in this way in the western United States (Leary et al. 1993); hybrid individuals rarely backcross to either parental species.

Sometimes the actions of one introduced species worsen the impact of others (Simberloff and Von Holle 1999). For example, the zebra mussel, by its prodigious water filtration, increases water clarity and thus aids the invasion of several introduced macrophytes, such as Eurasian watermilfoil (*Myriophyllum spicatum*). The increased growth of the macrophytes, in turn, aids the mussel by providing settling substrate (MacIsaac 1996). In other instances, highly coevolved species (that alone would be innocuous) produce, in concert, a damaging invasion, as witness the sudden spread of exotic fig trees (*Ficus* spp.) from Miami into Everglades National Park after the arrival of obligatory fig wasp (Hymenoptera: Agaonidae) pollinators (Kauffman et al. 1991).

WHAT TO DO—POLICY

In an era when free trade is almost a religion and amounts of travel and cargo are rapidly increasing, it will be difficult to attempt to introduce impediments and barriers to movement of species. However, one of the most important policy arenas is the World Trade Organization (WTO). The WTO Agreement on the Application of Sanitary and Phytosanitary Measures states that all new trade items, trade routes, or transportation methods are acceptable until they are proven to be too risky. This is called the "presumption of admissibility." The International Plant Protection Convention was revised to be in accord with the WTO Agreement in 1997.

The guiding philosophy of the WTO is that of a blacklist law. Anything may be imported unless it is on a blacklist of prohibited species. However, blacklist laws have never worked well to control introduced species (Simberloff 2000). It is difficult to get a species on a blacklist unless it has already caused damage, and by then it is usually too late because the great majority of established introductions are irrevocable. The WTO Appellate Body recently ruled against the Australian government in a salmon import case along these lines (Low 1999). The Appellate Body demands formal risk assessments and explicitly rejected scientific uncertainty about a risk as an adequate basis to preclude entry. However, risk assessments for introduced species are in their infancy, and there are several aspects of biology (such as evolution and autonomous dispersal) that make it extremely difficult to predict the trajectory of invasions (Simberloff and Alexander 1998). In other words, as a party to the WTO, if the United States wanted to adopt a broad ban such as, "no untreated wood or wood products unless the party proposing the import demonstrates no risk," they could be turned down on the grounds that this is protectionism. An appeal would have to be based on a risk assessment that presently cannot be done well and may always have a huge margin of error. It is worth noting that wooden packing material is believed to be responsible for the recent arrival of the Asian long-horned beetle (*Anoplophora glabripennis*) in New York and Chicago.

What is needed is a change in philosophy, away from innocent until proven guilty. The WTO must recognize that the very nature of introduced species makes current risk assessments unreliable documents, that introductions are generally irrevocable once they are established, and that the harm some species can cause is not only staggering in economic terms but incalculable in ecological ones. The United States, of course, has enormous influence on the WTO, but the leadership will have to come from the top—the President and the federal trade representative. What is really needed is a combination of a white list law (Ruesink et al. 1995) and a blacklist law; certain products and species are so inherently dangerous that they should be prohibited under any circumstances, while others (the vast majority) must all be subjected to detailed expert examination before they are put on an approved white list. That is, a precautionary principle is needed for introduced species.

The Convention on Biodiversity, held in Rio de Janeiro in 1992, specifically called for preventing introduction of species (article 8h): each contracting party shall "as far as possible and as appropriate . . . prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species." The United States, unfortunately, has not yet ratified the Convention, but ca 180 nations have, and this United States shortcoming will probably be remedied some day. Another problem is that article 8h has never really been made an action item for the Conference of Parties to the Convention (Glowka and de Klemm 1996); but this is simply a matter of building international interest in the problem. An extremely promising development is the growth of the Global Invasive Species Program (GISP), a component of an international program on the science of biodiversity (DIVERSITAS). GISP is coordinated by the Scientific Committee on Problems of the Environment in conjunction with the International Union for the Conservation of Nature, the United Nations Environment Program, and Commonwealth Agricultural Bureau International. In the last 3 years, GISP has sponsored an increasing number of workshops on many aspects of the introduced species problem, with emphasis on practical matters such as exclusion and management (Mooney 1999). This degree of high-level international activity may help to shift the direction of the WTO and other multilateral organizations.

Within the United States, many of the same problems arise as one finds on the international scene. For example, it is quite difficult for states to exclude a species they think might be a risk (e.g., bait or game fish, biocontrol agents), as the U.S. Supreme Court has usually called such exclusion an infringement of interstate commerce and therefore unconstitutional. However, a species from one part of the United States, even a native, can be extremely damaging in other parts of the United States where it is nonindigenous. East coast cordgrass (*Spartina alterniflora*) is a huge problem on California and Washington beaches (Daehler and Strong 1996). On ecological grounds, it is illogical for a nation as large as the United States to act as if a species native to one region is native to all.

At the federal level, Executive Order 13112 of 3 February 1999 on introduced species is a promising start at bringing about major changes in the way the United States deals with invaders. Currently, we operate largely by federal blacklists, such as the Federal Noxious Weed List. Species not on a blacklist (the vast majority of all species) are generally permitted entry into the United States. The primary agency in the United States charged with governing import of species, the United States Department of Agriculture Animal and Plant Health Inspection Service, currently operates without clear guidance on what should be quarantined, and it has recently relaxed controls on immigration of woody plants. The aforementioned executive order, sections 2.2 and 2.3, enjoins all federal agencies to prevent the introduction of invasive species and not to authorize or carry out actions that it believes are likely to cause or promote the introduction of invasive species, unless it has determined that the benefits of such actions clearly outweigh the potential harm. It will be interesting to see how these injunctions affect the overall flow of living organisms into the United States.

Executive Order 13112 also sets up an Invasive Species Council of the federal agencies. This council took a long time to initiate work, but by July 2000 it had established its expert advisory committee and produced a draft of a comprehensive management plan. The council has the prestige and scope to do much that is needed. The executive order is explicit only about federal activities, demanding a report from the council on what they are and how to improve them within 18 months. It has only inspirational language with respect to the states, municipalities, and private property owners, who are every bit as crucial in this battle. However, the council could be instrumental in generating the necessary coordination.

Both exclusion and management of introduced species could be greatly improved by increased cooperation between various entities managing nonindigenous species. On the management side, there is insufficient overall prioritization, and many agencies lack sufficient tools even to predict which invaders are likely to be problems. The National Park Service has a ranking system for plants (Hiebert and Stubbendieck 1993), while the Nature Conservancy has another one (Randall et al. 1996), the State of Washington uses yet a 3rd (S. Reichard personal communication), which one of the largest horticulture firms in this country claims to use voluntarily (Klinkenborg 1999), and the Australian government uses yet another one (Pheloung 1995). For animals, there really are no comparable tools. There is little retrospective research on how any of these tools for plants is working. Until some order is brought to this area and the scope is expanded, there will be no consensus on what to worry about and what to ignore.

Much more cooperation is also needed. For instance, we cannot have a situation that occurred in July 1999 (Barnard 1999). The Oregon Department of Agriculture had been trying for years to control Scotch broom (*Cytisus scoparius*), a weed that infests over 6 million ha in western Oregon. They had tried backhoes, root wrenches, and herbicides with little success. Finally, they found what they considered a promising biological control: European beetle (*Bruchidius villosus*) that eats seeds of Scotch broom. By 1999 they had reared enough individuals for a field test. At 1 of 12 sites, they released 250 beetles. A few days later a road crew of the Bureau of Land Management ripped out the entire Scotch broom patch and killed all the beetles. This case is emblematic; in the information age, there can surely be better organization and cooperation. There has to be more readily accessible and comprehensive data on which species are where, what they are doing, and which agencies are doing what where (Ricciardi et al. 2000). Information on successful and unsuccessful management techniques should be much more widely disseminated.

The biggest improvement of all, from both national and international standpoints, must come from increased public pressure. The battle against invaders can be won. All techniques in use can be improved, and coordination will enhance success. The key is for the public to pressure policymakers to ensure creation of an improved legal and operational framework.

WHAT TO DO—MANAGEMENT

Both in the United States and worldwide, many invaders have been eradicated completely (Simberloff 1997, 2000). Most had inhabited only small areas (e.g., Asian wild rice [*Oryza rufipogon*] in a 0.1-ha area of Everglades National Park), but several were well established over wide ranges. For example, the African malaria mosquito (*Anopheles gambiae*) was eradicated from over 30,000 km^2 in northeastern Brazil (Davis and Garcia 1989). The probability of successful eradication is enhanced if a species is detected early in the invasion and eradication efforts begin quickly. However, such efficiency requires either great luck or a good monitoring program and a rapid response mechanism. Other factors conducive to successful eradication include a thorough understanding of the biology of the target organism, sufficient resources to carry the project to completion, and the regulatory power to enforce cooperation in such matters as quarantines.

If eradication fails or is not attempted, there are 4 basic control approaches, and for the first 3 there have been some striking successes, as well as crushing failures (Simberloff et al. 1997, Simberloff 2000). First, mechanical means as simple as hand-picking and as complicated as elaborate machinery can control certain species at acceptably low densities. Volunteer labor has frequently been used in such efforts, as has convict labor. Second, chemical means (i.e., herbicides, rodenticides, insecticides, etc.) are sometimes effective, although they are often controversial. Some early-generation pesticides had substantial nontarget impacts, including human health effects, and these problems have left a legacy of chemophobia in some circles (Williams 1997). Even though many current chemical controls have few if any nontarget impacts, there are other disadvantages. First, many are expensive, particularly if they are to be used routinely over large natural areas. Second, species evolve resistance to them, which both increases the cost and means that no chemical can be used in perpetuity.

The 3rd approach, biological control, is often seen as a green alternative to chemical control. In some instances it has worked superbly (e.g., the control of South American alligatorweed [*Alternanthera phyloxeroides*] in Florida by the flea-beetle *Agasicles hygrophila* [Center et al. 1997]), with the pest kept in check at a relatively constant low density in homeostatic fashion by its natural enemy. However, biological control has recently come under critical scrutiny. First, it usually does not work; that is, the target pest is usually not substantially reduced. However, about 3 times as many introduced biological control agents establish populations as effect substantial control (data in Williamson [1996]). Second, in some instances, biological control agents have attacked nontarget species, and they have even driven some to extinction (Simberloff and Stiling 1996, and references therein).

Finally, management of an entire ecosystem can sometimes create conditions inimical to introduced species but suitable for the natives. Consider the forests of the southeastern United States dominated by longleaf pine (*Pinus palustris*). These forests formerly extended over 28 million ha. Less than 600 ha of old growth remains, but there are substantial amounts of 2nd growth with varying degrees of similarity to the original forests. Longleaf pine forests are classical fire disclimaxes (Hermann 1993); they are maintained by cool, growing-season fires, usually every 2–5 years, and the longleaf pine itself, groundcover plants (often dominated by wiregrass [*Aristida* spp.]), and all other inhabitants are adapted to thrive in such a fire regime. It is striking that, when a natural fire regime is maintained, this community is barely invaded, even though the Southeast has more than its share of nonindigenous species. The red imported fire ant, though wreaking havoc in much of the Southeast (Tschinkel 1993), does not get into intact longleaf pine forest except along roads (McInnes 1994); a native fire ant (*S. geminata*) persists here, though the invader replaces it in other habitats. Similarly, the plant community notably lacks invaders. In the largest old-growth longleaf pine forest (80-ha Wade Tract in south Georgia), there are few introduced plants, though these are worrisome because nearby areas are increasingly converted to suburban housing with exotic landscaping. The groundcover of the Wade Tract has almost 400 species of native plants. There are about 11 nonindigenous plant species (S. Hermann personal communication), and almost all individuals are within 2 m of human disturbance, especially the old trails that dissect the fragment. There are approximately 22 other nonindigenous plants within 200 m of the Wade Tract, but they have not invaded. The apparent resistance to invasion probably has to do with the frequent fires that destroy the exotics except on the trails, which rarely burn. If a fire-adapted nonindigenous species such as Asian cogon grass (*Imperata cylindrica*) were to colonize this region, the Wade Tract might be invaded. However, to date, it seems as if the prescribed burns, more or less mimicking the natural fire regime, have controlled invasive species in this forest.

Ecosystem management, though adopted by virtually all federal agencies as the operative means of managing natural resources, has largely been a catch-phrase rather than a group of well-defined and tested techniques (Simberloff 1998). Whether longleaf pine forests are unusual in that a particular management tool (routine growing season fires) tends to maintain an entire ecosystem remains to be seen. There may be other communities that can be kept largely intact in the face of potential invaders by managing entire ecosystems.

Because it is the newest approach, ecosystem management is most in need of enhanced research. But all of the approaches—eradication plus mechanical, chemical, and biological control—could be greatly enhanced by substantial research. First, much management literature is very gray. Some management techniques are transmitted only verbally. Thus, wheels are probably continually reinvented, even some that failed to work the first time. Again, in an age of information transfer, this should not happen. As introduced species databases are improved and become increasingly user-friendly and compatible with one another (Simberloff 1999), it is important that management techniques and attempts be part of the easily accessible record. Second, much basic research is required on all management techniques. As I stated at the outset, all are characterized by some successes and some failures, and there is little doubt that percentages of the former can be increased by well-designed, traditional research.

CONCLUSIONS

An aura of hopelessness sometimes surrounds the issue of introduced species, as if an increasing flood of invaders is inevitable and our potential arsenal to limit their entry and impact is meagre (Quammen 1998). Although the battle to manage this problem adequately will be long and difficult, there are 2 reasons not to surrender. First, if the public gives up, many habitats will surely progressively drown in a sea of exotics, and much of the Earth, national parks included, will indeed become a "planet of weeds" (Quammen 1998). Second, many things can be done to improve the response to this assault. On the policy front, a shift from a blacklist philosophy to a combination of white lists and blacklists would drastically reduce the number of nonindigenous species that would actually invade any nation, and perhaps even parts of large nations. Coordination and cooperation on many fronts seem logistically feasible, if sufficient resources are devoted to this problem. Areas in which coordination would greatly improve the current situation are monitoring, risk assessments and prioritization procedures, rapid response teams, reporting of attempted management procedures, and availability of basic biological data on introduced species.

Further, various procedures already used for management could all be greatly improved. With increased monitoring, an appropriate rapid response mechanism, and technological improvements in methods of attack, a major increase could be achieved in the rate at which nonindigenous species are eradicated before they are widespread or even established. For established pests, although ecosystem management is probably most in need of substantial research as a tool to exclude exotics, the more traditional methods—mechanical, chemical, and biological control—could all be enhanced in terms of both efficacy in eliminating the target pests and minimization of nontarget impacts. In light of the striking successes that each of these methods (and combinations of them) has already achieved, with a relatively small research effort compared to that in, say, public health or pollution control, there is reason for optimism that major technological advances in all of them could make vast strides toward bringing the introduced species problem under control.

What will be required to achieve these improvements in policy and technology? Public pressure! As the public increasingly recognizes the terrible cost imposed by nonindigenous species, they will demand more effective action to do something about this problem. And when the public demands action, they will get it.

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A PALEOECOLOGIC PERSPECTIVE ON PAST PLANT INVASIONS IN YELLOWSTONE

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ABSTRACT.—The role of climate and natural disturbance in the past provides a context for understanding present and future changes in biota. The vegetation history of the Yellowstone region, like that of North America as a whole, is largely one of plant invasions and extinctions in response to changes in climate and environment. When Holocene plant migrations are examined on multiple spatial and temporal scales, several generalities are apparent. First, at a continental and regional scale, plant migration patterns followed the direction of climate change, whereas at local scales plant colonization was governed by site-specific conditions and possibly by biotic interactions. Second, species were individualistic in their response to climate change, and, as their ranges shifted across the landscape, existing communities were dismantled and new ones were formed. Individual species met little resistance from existing communities. Third, rates of species invasion were astonishingly rapid, suggesting that rare long-distance dispersal events were critical. Fourth, fire during periods of climate change was an important catalyst in allowing the invasion of new species, but it is unlikely that a single fire event triggered irreversible vegetation change.

Regional climate and biotic changes in response to projected increases in atmospheric CO_2 in the next century suggest an even more complex picture than in the past. Model simulations portray changes in temperature and precipitation in the Yellowstone region that have not occurred in the last 20,000 years. Likewise, projected changes in species ranges, including latitudinal, longitudinal, and elevational shifts, require faster rates than anything observed in the fossil record. Increased fire occurrence may help maintain some native taxa but promote the decline of others. Thus, future conditions are likely to create evermore opportunities for exotic species to invade and establish within the Yellowstone region.

Key words: Yellowstone, past plant migrations, paleoecology, fire history, invasive species.

> Exotic species are those that occur in a given place as a result of direct or indirect, deliberate or accidental action by humans (not including deliberate reintroduction). . . . The exotic species introduced because of such human actions would not have evolved with the species native to the place in question, and, therefore, would not be a natural component of the ecological system characteristic of the place (National Park Service 1988).

This definition of exotic species emphasizes the fact that human actions are responsible for the introduction of new species that pose considerable threat to the health of native ecosystems. The definition also implicitly raises questions about the natural state of ecosystems on long time scales and the relative importance of biotic invasions and range expansions prior to extensive Euro-American activity. To address these issues requires an examination of the paleoecological record, inasmuch as such data disclose the response of biota in the face of past environmental changes (Millar and Woolfenden 1999) and provide a natural baseline against which to measure present conditions (Swetnam et al. 1999). A long-term perspective also allows us to consider the role of climate and natural disturbance in accomplishing major biogeographic changes. Paleoecologic data thus offer a context by which to evaluate present invasions and their ecological consequences.

Information on past changes in species distributions is also relevant in assessing the potential impact of rising concentrations of atmospheric CO_2 and other "greenhouse" gases on ecosystems in the future. Land managers around the world are engaged in complicated and expensive efforts to combat the introduction and expansion of alien species, and several studies have noted that projected climate changes will accelerate the success of these invasions (e.g., Vitousek et al. 1996, Dukes and Mooney 1999, Mooney and Hofgaard 1999). Rates of exotic species spread are alarming, particularly in areas of highly altered habitat and human-mediated disturbance, but even

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seemingly pristine places, like Yellowstone National Park, are not immune to the assault. At present, over 170 species of nonnative plants have been identified in Yellowstone, and additional invasions are imminent (Olliff et al. 2001, Whipple 2001).

The objectives of this paper are to (1) provide some examples of past plant migrations in North America and Europe, as well as in the Yellowstone region, during the Holocene (the last 10,000 years of earth history), (2) describe the role of natural disturbance as a trigger of past vegetation change, and (3) compare past and present biogeographic changes in Yellowstone with projections of ecosystem changes in the future.

BIOTIC INVASIONS IN THE PAST

Pattern of Plant Migrations

An "invasive species" has been defined as one whose introduction does or is likely to cause economic or environmental harm or harm to human health (President's Executive Order EO13112 of February 3, 1999). Certainly, this narrow definition does not fit the spread of native species in the past, but current invasions and past "migrations" both require species to colonize, establish, and reproduce in new plant communities. The paleoecologic record therefore offers insights into the ecological consequences of introducing new species into established communities, as well as the potential rate of species spread.

The paleoecologic record of the last 20,000 years provides evidence of significant adjustments in the geographic distribution of plants and animals since the last ice age. These biogeographic changes involved displacements that ranged from a few to hundreds of kilometers (see Webb et al. 1983, Huntley 1988, Webb 1988, Elias 1991, FAUNMAP Working Group 1996), and they were accomplished by a series of biological invasions in which new species moved into and potentially disrupted existing ecosystems. The paleoecologic record indicates that species were highly individualistic in the direction and rate of migration because each had particular environmental requirements that dictated their pattern of colonization. As a result, the ranges of species shifted in no single direction, and communities were continually formed and dismantled in the process. To accomplish the long-term patterns of migration, the rates of invasion for most species were breathtakingly fast, e.g., on the order of 200–1500 m · yr^{-1} for major tree taxa (Huntley 1988, Birks 1989). Long-distance dispersal was apparently critical in the past, and the process was probably similar to exotic species invasions in this century that begin with a quiescent phase of little discernible range change and are followed by an active phase of explosive expansion (Mack 1986, Pitelka et al. 1997).

The large-scale picture of past tree invasions comes from examining networks of radiocarbon-dated pollen records. One approach for analyzing pollen data is to determine the timing of the first appearance of species at individual pollen sites and compile these "first appearance" dates to construct a map of range limits for different time intervals (pollen isochrone maps; see Davis 1981a, 1983, Gaudreau and Webb 1985). Another approach is to plot the abundance of particular pollen types at specific locations and develop pollen percentage contour maps (isopoll maps; see Huntley and Birks 1983, Webb et al. 1983, Bartlein et al. 1986, Huntley 1988, Webb 1988). Changes in the spatial patterns of pollen abundance are then used to track the distribution of the species at different times.

The pollen record of spruce in North America and Europe provides an example of the range shifts that occurred in the last 18,000 years[2] (Webb and Bartlein 1992; Fig. 1). In North America a network of pollen records indicates that spruce (*Picea glauca* and *P. mariana*) resided in the southern and central Great Plains during the last ice age. As the climate warmed, spruce shifted its range northward and eastward into deglaciated regions. By 12,000 years ago, it occupied a broad region along the southern margin of the retreating ice sheet. The advance of spruce in interior Canada was particularly rapid from 12,000 to 9000 years ago and has been attributed to strong southeasterly winds off the ice sheet that may have transported seeds exceptional distances (Ritchie and MacDonald 1986). At 6000 years ago, the northern limit of spruce lay north of its present position as a result of higher-than-

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[2] Ages are given in radiocarbon year, except where noted, because most of the literature cited uses radiocarbon year. Radiocarbon ages depart from true calendar year for some periods of the Holocene (Stuiver et al. 1998) and affect calculation of rates of change. The general picture of invasion is unchanged by using radiocarbon dates; however, the rates of change are different.

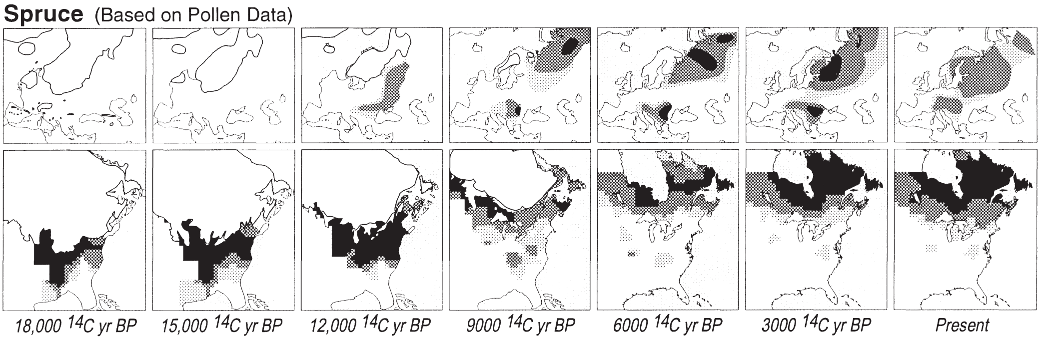

Fig. 1. Geographic variations in the abundance of spruce (*Picea*) pollen in Europe (top row) and eastern North America (bottom row). Darkest shading represents >20% spruce, medium shading represents 5–20%, and light shading represents <1% (after Webb and Bartlein 1992).

present temperatures. In the last 6000 years, the limit of spruce has shifted southward because of cooler conditions. The modern boreal forest formed in only the last 3000 years when the ranges of white spruce (*Picea glauca*), black spruce (*P. mariana*), jack pine (*Pinus banksiana*), tamarack (*Larix laricina*), and balsam fir (*Abies balsamifera*) overlapped. The present distribution of boreal mammals was also attained at this time (FAUNMAP Working Group 1996). In Europe, Norway spruce (*Picea abies*) moved from its glacial range in northwestern Russia westward into Fennoscandia and eventually into the Baltic region and Sweden. Some researchers have suggested late-Holoceme deforestation as the cause of the spruce expansion in Fennoscandia; however, climate-model results indicating lower winter temperatures and increased winter precipitation may better explain the pattern (Huntley 1988).

An example of a prehistoric pathogen invasion that had large ecological consequences comes from eastern North America. The invasion occurred 4650 ± 300 years ago when forests of hardwoods and conifers extended across the eastern and central U.S. (Gaudreau and Webb 1985). At this time populations of eastern hemlock (*Tsuga canadensis*) declined precipitously in the forest, as evidenced by the sharp drop in hemlock pollen percentages at most sites. The demise was rapid, widespread, and showed no discernible geographic pattern. Hemlock was the only victim detected in the fossil record, but organisms that relied on hemlock probably also declined. Davis (1981b) attributed the “hemlock decline” to the effects of a pathogen, not unlike the European chestnut blight of the 1900–1920s that killed American chestnut (*Castanea dentata*) in the same forests. Competing theories, such as climate change or widespread natural disturbance, do not adequately account for the abrupt decline of a single species over such a large area. A recent study (Bhiry and Filion 1996) suggests that a series of defoliating events between 4900 and 4200 years ago led to the loss of hemlock; hemlock looper (*Lambdina fiscellaria*) and other lepidopteran defoliators, including spruce budworm (*Choristoneura fumiferana*), were the likely culprits. These insects have their greatest impact during warm, dry conditions, as was the case at the time of the hemlock decline.

How long did it take for hemlock to recover following its decline? Pollen records suggest 500–1000 years, but forests in most places were never the same (Davis 1981b). In the absence of hemlock, tree species like maple (*Acer*) and beech (*Fagus*) expanded their range and presumably took over the ecological space occupied by hemlock. Moreover, the climate 1000 years later was cooler in many areas than it had been before, and this probably shifted the ecological balance (Bartlein et al. 1986). Although hemlock survives to the present, one could argue that the legacy of the pathogen(s) is still evident.

When past invasions are examined at the local scale, the pattern of colonization seems to be shaped by the interplay of soil characteristics and disturbance regimes at the site level and the overarching control of climate at the regional scale (Brubaker 1975, Graumlich and

Davis 1993, Davis et al. 1994). Stratigraphic changes evident in individual pollen diagrams suggest that most sites experienced long periods of vegetation stability, which are designated as pollen zones, interrupted by periods of relatively rapid change, marked by pollen zone boundaries. Periods of invasion span 500–1000 years at most sites, whereas periods of relative stability often last for millennia (Watts 1973). The transition periods thus represent several generations of the invading species, which implies that past invasions of native tree taxa were gradual but fairly opportunistic events. A species' success depended on the ability of seedlings to establish and survive during a phase of initial low population density. Stable populations within the existing communities seem to have offered little resistance to these tree invasions; instead, the important controls appear to be habitat conditions and intraspecific biological constraints (Watts 1973).

Opportunism modulated by habitat conditions is also evident on longer time scales when the vegetation history of other interglacial periods is examined. In northeastern Europe, for example, subtle variations in the sequence and direction of plant migrations distinguish each interglacial period and attest to the fact that plant associations are not persistent in time (Watts 1988). For example, *Abies* was more widespread and moved more rapidly in the Holsteinian interglacial period than in the younger Eemian or Holocene interglacial periods. Differences in migration history are attributed to variations in the location of glacial refugial populations and the climate of each interglacial period.

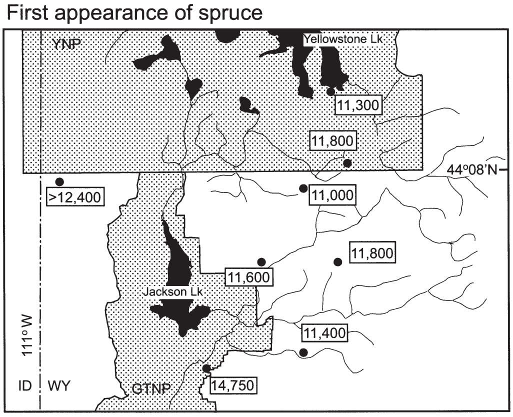

Fig. 2. Age (in radiocarbon years before present) of the first appearance of Engelmann spruce (*Picea engelmannii*) in Grand Teton National Park (GTNP) and southern Yellowstone National Park (YNP) based on the initial increase in *Picea* pollen in a network of pollen records. All sites lie within the area that was glaciated by the Yellowstone ice cap, and the center of glaciation was in the Yellowstone Lake region (after Whitlock 1993). Large lakes are shown in black.

In the western United States, the density of fossil sites is too sparse to describe the pattern of postglacial plant migrations in detail. Regional descriptions of vegetation history, however, are available from several regions, including the American Southwest (Betancourt et al. 1990), Pacific Northwest (Whitlock 1992), Colorado Rockies (Fall 1997), and Sierra Nevada (Anderson 1990). In the Yellowstone and Grand Teton region, a series of pollen records from the former ice margin to the center of glaciation (Whitlock 1993, Whitlock et al. 1995) provides information on the movement of conifers during deglaciation. For example, the spread of Engelmann spruce (*Picea engelmannii*) is estimated from the first increase in spruce pollen and presence of needles in a series of Yellowstone sites (Fig. 2). The evidence suggests that spruce survived close to the ice margin in northwestern Wyoming and southeastern Idaho, probably as small populations in protected areas. As the climate warmed and glaciers receded, the range of spruce shifted northward and eastward into northern Jackson Hole. Spruce was present in northern Jackson Hole by 14,750 years ago and reached the Yellowstone Lake region by about 11,300 years ago. The pattern of spruce invasion within the deglaciated region was not unidirectional, and elevation, soil development, and environmental conditions probably complicated colonization at the local scale. Nonetheless, a simple calculation of the invasion rate from its arrival at the former ice margin to its appearance near Yellowstone Lake (the former ice center) is $\sim 100 \text{ m} \cdot \text{yr}^{-1}$, which is consistent with rates estimated for spruce in eastern North America and Europe (Davis 1981a, Huntley 1988). Although pace of climate change and availability of suitable habitats limited the migration of all, the similarity among widely separated species of *Picea* is remarkable. It suggests that spruce may have an intrinsic rate of response determined by its biological constraints to produce and disperse seeds, establish seedlings and saplings, and grow to reproductive age. If so, this characteristic has probably been acquired as part of a long-term evolutionary strategy for surviving the climate changes that accompany glacial/interglacial cycles (Barnosky 1987, Bartlein 1997, Bennett 1997, Jackson and Overpeck 2000).

Several plant species in the western United States have experienced recent expansions that may be either a continuation of Holocene range changes or a response to recent human activities (Swetnam et al. 1999). The appearance of pinyon pine in northern Colorado 400–500 years ago, for example, seems to be a part of a general expansion from Mexico that has been underway since the last ice age (Betancourt et al. 1991). Climate change has also been implicated in the recent spread of creosote bush (*Larrea tridentata*) in the middle Rio Grande Basin and Borderlands of Arizona and New Mexico (Grover and Musick 1990), single needle pinyon (*Pinus monophylla*) in northern Nevada (Nowak et al. 1994), Utah juniper (*Juniperus osteosperma*) in Wyoming (Swetnam et al. 1999), and western juniper (*Juniperus occidentalis*) in eastern Oregon, (Miller and Wigand 1994, Miller and Rose 1995). Paleoecologic data show that these taxa have undergone considerable adjustment in their ranges during the Holocene and may still be migrating in response to long-term climate changes. However, the impact of such Euro-American activities as grazing, agriculture, and fire suppression on their recent spread is difficult to disentangle from the impact of longer processes.

Importance of Natural Disturbance

Disturbance, particularly fire, is considered an important catalyst in the spread of exotic species at present (Vitousek et al. 1996). Exotic grassland species, for example, have been shown to initiate and maintain a fire regime that prevents the regeneration of native woody and grassland species (D'Antonio and Vitousek 1992). Paleoecologic records, on the other hand, suggest that fires have been a major form of natural disturbance in temperate ecosystems throughout the Holocene and have helped maintain particular vegetation types for long periods. Such records also show that the frequency and ecological importance of fires have varied in association with past climate changes (see Clark et al. 1996, Millspaugh et al. 2000, Whitlock and Larsen in press).

Yellowstone National Park is one location where climate-vegetation-fire relationships have been studied on both short and long time scales, and thus the role of fire in biotic change can be assessed. Fire reconstructions of the last 500 years come from dendrochronological records (Romme and Despain 1989, Barrett 1994), including fire-scarred tree-ring data and forest-stand ages. Holocene records of fire occurrence are available from high-resolution charcoal records obtained from lake sediments (Millspaugh and Whitlock 1995, Millspaugh et al. 2000[3]. Both tree-ring and charcoal data indicate that a combination of small, frequent fires and large, infrequent fires characterizes the current fire regime. For example, the period from 1690 to 1750 A.D. experienced extensive fires, but several decades with small or no fires followed it. This regime led to the development of extensive old-growth forest in the late 20th century and large accumulations of burnable biomass. Unusual weather and fuel conditions triggered large fires in 1988, which affected 395,600 ha of the park (Schullery 1989, Balling et al. 1992). Although these fires have no precedence in recorded history, they seem to be well within the natural range of variation documented in the dendrochronological and charcoal record.

Long charcoal records from Yellowstone reveal the relationship between fire, vegetation, and climate on millennial time scales (Fig. 3). At Cygnet Lake in the Central Plateau region, a sharp increase in fire frequency occurred at the beginning of the Holocene. The change in fire regime coincided with the onset of warm conditions and the establishment of lodgepole pine forest in an area that was previously covered by tundra vegetation. Local fires were most frequent between 11,000 and 7000 years ago[4] (>10 fires $\cdot$ 1000 yr^{-1}). Paleoenvironmental records from southern and central Yellowstone and Grand Teton national parks suggest that summer temperatures were higher than today and drought was more severe at this time (Millspaugh et al. 2000). Fire occurrence decreased to the present frequency of

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[3] Charcoal analysis is based on evidence that charcoal particles are introduced to lakes during and shortly after a fire. Sedimentary layers with abundant large charcoal particles provide a record of past fire events in the watershed (Whitlock and Millspaugh 1996, Whitlock and Larsen in press). In a study of 4 small lakes, charcoal peaks dated by the lead-210 method matched well with timing of fires identified by historic documents and dendrochronologic studies (Millspaugh and Whitlock 1995).

[4] These dates are given in calendar year (see Millspaugh 1997).

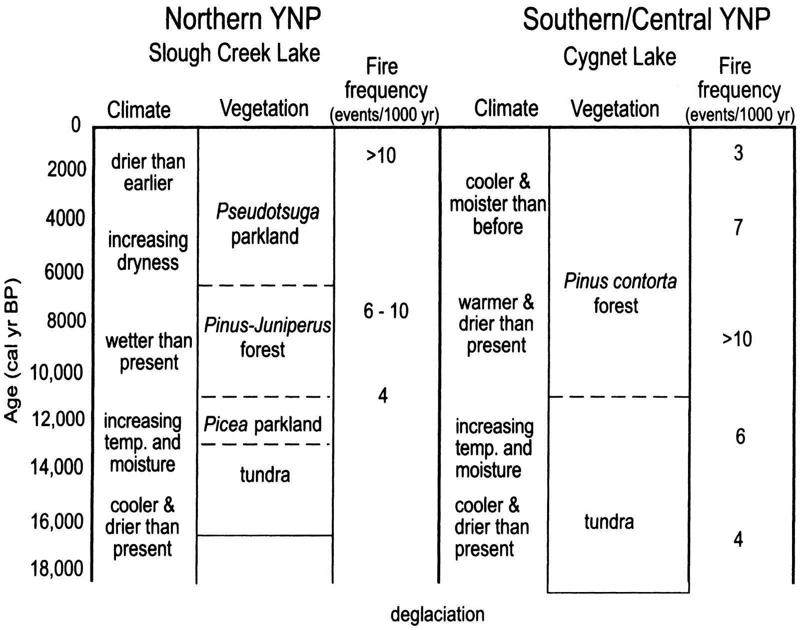

Fig. 3. Comparison of climate, vegetation, and fire history in 2 regions of Yellowstone with contrasting Holocene climate histories (after Millspaugh 1997). Ages in this figure represent calendar years before present.

2–3 · 1000 yr^{-1} in the last 7000 years as the climate become cooler and wetter. Despite these changes in fire regime and climate, the forest continued to be dominated by lodgepole pine, probably because the infertile soils of the Central Plateau have limited the establishment of other conifers (Whitlock 1993).

Pollen and charcoal data from Slough Creek Lake in northern Yellowstone, in contrast, show changes in both vegetation and fire regime as a result of Holocene climatic change. A period of pine-juniper (*Pinus-Juniperus*) forest and low fire frequency occurred between 11,000 and 7000 years ago, when the climate was warmer and wetter than present. Wetter-than-present conditions in this region have been attributed to a strengthening of summer monsoonal circulation in the early Holocene (Whitlock and Bartlein 1993). Fire frequency has increased from 4 fires · 1000 yr^{-1} to >10 fires · 1000 yr^{-1} in the last 7000 years, and Douglas-fir (*Pseudotsuga menziesii*) parkland has established as a result of cooler, drier conditions and increased fire activity (Millspaugh 1997).

A comparison of the Cygnet and Slough Creek records on a finer time scale reveals short periods when both sites burned despite their long-term climate differences; 1988 was such a year, and another period occurred about 1000 years ago during a warm, dry interval known as the Medieval Warm Period (Millspaugh 1997). At these times, short-term climate variations apparently overrode the influence of the slowly varying climate changes and led to fires in both summer-wet and summer-dry regions. The pollen record suggests that such short-term variations are not accompanied by major changes in vegetation composition or by the appearance of new species.

General Observations

Past changes in the ranges of native taxa invite a few comparisons with the spread of exotic species at present (Table 1).

First, plant migrations on long time scales have been governed primarily by climate change and the attendant effect of climate on the physical and biotic environment (Bartlein et al. 1986). In contrast, exotic species invasions at present are largely determined by the direct and indirect actions of humans. This difference contributes to the unprecedented nature of current invasions.

Second, the pattern and rate of invasion vary among species. The paleoecological record

TABLE 1. Characteristics of biological invasion: past, present, and future.

	Holocene time scales	Last few centuries	Next century
Mode of dispersal	irrelevant	human, wind, animal vectors	human (dispersal may require deliberate assistance)
Rate of movement[a]	<1 km · yr^{-1}	>10 km · yr^{-1}	>40–50 km · yr^{-1}
Primary cause of invasion	climate change	human activities	climate/human activities
Proximal cause of invasion	natural disturbance	natural and human disturbance	natural and human disturbance
Limits to invasion	major biogeographic barriers (mountain ranges, oceans, deserts)	characteristics of invading species, human activities, landscape pattern	uncertain

[a]Based on Mack 1986, Huntley 1988, Webb 1988, Bartlein et al. 1997

from Yellowstone and elsewhere suggests that species adjusted their range during the Holocene according to their individual requirements. Features such as soil and disturbance regime helped guide the local pattern of invasion, but, at regional and continental scales, climate conditions governed species limits. Physical barriers have not been significant obstacles to invasion in the past or at present. The Great Lakes and the deserts and mountains of the western United States did not slow climatic-driven Holocene plant migrations in North America (Thompson 1988, Betancourt et al. 1990, Davis et al. 1994). Likewise, mountain ranges, deserts, and oceans have been easily breached by exotic species in recent times as a result of human-assisted dispersal (Vitousek et al. 1996, Cox 1999, Mack et al. 2000).

Third, much debate focuses on the significance of species richness and community structure on the invasibility of present-day communities (Elton 1958, Tilman and Downing 1994, Stohlgren et al. 1999, Levine 2000). On long time scales these attributes seem to have little importance because patterns of plant migration at continental and even local scales have been strongly mediated by environmental conditions (Davis et al. 1994). Indeed, paleoecological records indicate that invading species meet little resistance from existing ones. As a result, communities have been dismantled and reorganized continually through the Holocene. The observation that present-day communities have no long history suggests that species richness and structural complexity may ultimately prove irrelevant to the success of exotic species.

Fourth, the ecological mechanisms that enable most tree taxa to move presently operate too slowly to account for the rates of movement observed on Holocene time scales (Huntley 1988, Birks 1989, Clark et al. 1998; Table 1). This mismatch between present and past observations points to the importance of rare events, including long-distance dispersal, in shaping present-day geographic distributions (Cox and Moore 2000). Waif dispersal is a poorly understood process in modern ecology; yet, it may be key in explaining major expansions in geographic range over the long term (Clark et al. 1998).

Finally, paleoecological records clearly show that climate, fire, and vegetation are interrelated elements of the earth system, and their variation and interaction through time have shaped the modern landscape. On century and millennial temporal scales, large changes in climate determine fire regime and vegetation composition. Yellowstone studies indicate that periods of major climate change, such as transitions from the late-glacial period to Holocene and the early Holocene to late Holocene, were accompanied by changes in fire frequency. This shift in fire regime undoubtedly contributed to vegetation changes recorded in the pollen records of specific sites. In the absence of climate change, fires should be considered an intrinsic component of the ecosystem, whereas during periods of climate change, fires are significant catalysts that allow the invasion of new species. The role of fire at present is further accentuated by nonclimatic disturbances, such as human-caused habitat alteration and landscape fragmentation.

BIOTIC INVASIONS IN THE FUTURE

An issue of great concern and debate is how past and current species invasions compare with those that may occur in the future (Vitousek et al. 1996, Pitelka et al. 1997, Dukes and Mooney 1999, Davis and Shaw 2001). Efforts to address this question rely on results of climate and ecological model simulations that examine ecosystem responses under elevated greenhouse gases (Houghton et al. 1996). In the western United States, atmospheric general circulation models (AGCMs) and regional climate models have been used to compare changes in climate arising from a doubling of atmospheric carbon dioxide (referred to as the $2xCO_2$ climate) with those simulated for the present day (Bartlein et al. 1997, Thompson et al. 1998). The output of climate models has also been introduced into ecological models to consider the response of particular taxa to changes in seasonal and annual temperature and precipitation. Comparison of present and future species ranges identifies where suitable habitat will be lost, gained, or remain unchanged in the future. These projected range changes, like those in climate, represent a comparison of equilibrium conditions (i.e., how the species ranges or regional climate in a $2xCO_2$ climate compares with simulations of present conditions).

Climate and ecological models are continually under refinement. AGCMs and regional climate models improve as spatial resolution, physics of atmospheric circulation, and interactions of the atmosphere and Earth's surface become better constrained. Ecological models are becoming more realistic by incorporating bioclimatic variables, such as growing degree days, minimum temperature, effective moisture, and the biophysical effects of CO_2 on plant growth. Nonetheless, model simulations should be considered projections of potential climate-vegetation relationships under equilibrium conditions; they are not predictions of what will actually occur.

Most climate projections of the future indicate warmer, wetter conditions in the northwestern United States (Bartlein et al. 1997, Thompson et al. 1998). Differences between $2xCO_2$ and present-day simulations in the Yellowstone region include an increase in January and July temperatures of more than ~5°C, a substantial increase in January precipitation, and less extreme and spatially more variable changes in July precipitation. Modern climate analogues for projected changes in the Yellowstone region are found in the interior Pacific Northwest, the Wasatch Range, and lower elevations of the Absaroka Range (Bartlein et al. 1997). Other model simulations suggest a greater role for fire in the future, both in terms of more convectional activity (Price and Rind 1994) and reduced water surpluses in summer (S. Shafer unpublished data 2000).

The location of suitable climate for particular species changes dramatically in future simulations, but, in general, low-elevation taxa are less impacted than high-elevation species (Bartlein et al. 1997). For example, the future range of low-elevation lodgepole pine (*Pinus contorta*) in Yellowstone is little changed from its present distribution (Fig. 4). The climate suitable for Douglas-fir, another low-elevation species, shifts to intermediate elevations in future simulations, probably because drought conditions at low elevations limit its growth.

In contrast, projected future conditions in most of Yellowstone and the Northern Rocky Mountains are not suitable for current high-elevation species. Whitebark pine (*Pinus albicaulis*) is a subalpine species that provides food for grizzly bear, Clarks Nutcracker, and red squirrel in Yellowstone (Despain 1990). Its range is nearly eliminated in Yellowstone in the $2xCO_2$ scenario. This keystone species has declined already with the spread of white pine blister rust (*Cronartium ribicola*) in the late 20th century (Kendall et al. 1999). The additional impact of projected climate changes on whitebark pine has not fully been considered in conservation plans aimed at protecting grizzly bear habitat.

Current models are not able to consider transient conditions that might determine whether species could keep pace with projected climate changes, nor do they address the importance of habitat connectivity, competition, and disturbance in influencing biotic responses. These factors will be critical in predicting the response of native and exotic species. For example, the attendant changes in fire regime toward more frequent and/or more intense fires will undoubtedly complicate vegetation adjustments. The ability of lodgepole pine to grow on infertile soils and reproduce following fire (neither of which is considered in model experiments) should help perpetuate

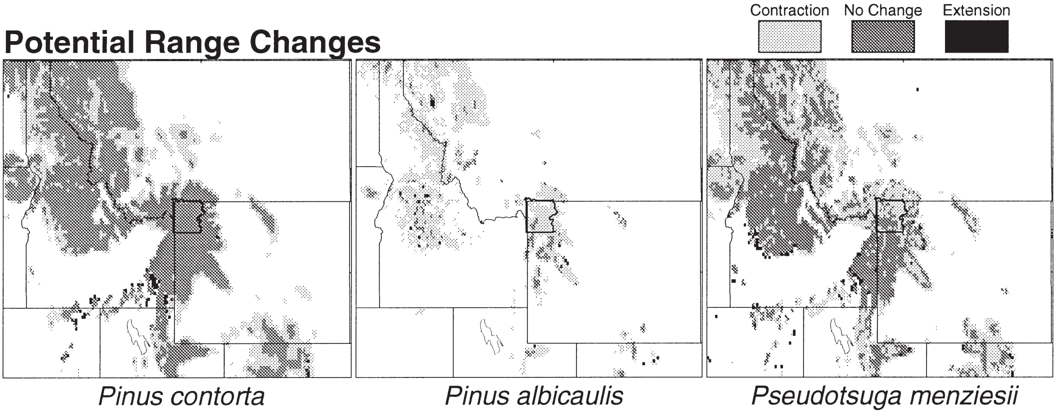

Fig. 4. Potential range changes for 3 tree taxa. Medium shading indicates grid points where a specific taxon occurs under both the present and $2xCO_2$ climate; light shading indicates grid points where a taxon occurs under the present climate, but does not occur under $2xCO_2$ climate; and dark shading indicates grid points where a taxon does not occur under the present climate, but is present under $2xCO_2$ climate conditions (after Bartlein et al. 1997).

it as a forest dominant in the future. Fires may also encourage the spread of Douglas-fir into new areas, since its seedlings require light and mineral soil to become established (Burns and Honkala 1990). On the other hand, the thick bark of mature Douglas-fir trees is an adaptation to fire, and increased fire occurrence may delay the decline of old-growth Douglas-fir forest and the invasion of new tree species. Fires will likely accelerate the decline of whitebark pine, given its sensitivity to intense fires. Added to this picture is the role of opportunistic exotic species that thrive in areas of disturbance.

The message of future climate studies for conservationists and land managers is not whether the simulations are correct in detail (they probably are not). Rather, the point is the model results consistently suggest that large biogeographic adjustments will be required if species are to maintain equilibrium with future climate conditions. Current simulations indicate complex changes in mountain regions that include north- and southward shifts as well as altitudinal adjustments of species ranges. The rates of movement required of species to keep pace with projected climate changes are greater than anything observed in the fossil record of the last 20,000 years. Predicted increases in fire frequency and intensity will affect species differently. A shift toward more frequent or intense fires will create ecological opportunities for some taxa, but, in other cases, fire may retard vegetation changes by helping to maintain existing communities.

CONCLUSIONS

The process of invasion looks different depending on whether one uses Holocene time scales, the last few centuries, or the next 100 years as the time scale of interest. The relative importance of biological versus climatic constraints on invasion also varies with time scale. When invasion is studied on long time scales, the specific mechanism of dispersal and the role of natural disturbance are generally unimportant because large-scale climate change is the primary driver. During the Holocene, rates of migration for most tree species were <1 km $\cdot$ yr^{-1}, and, although fire and other natural disturbances may have promoted invasion at the local scale, no single fire led to unidirectional ecological change.

Exotic plants in recent centuries have been largely introduced by the deliberate and accidental actions of humans, but their success as invaders is constrained by the characteristics of the species and habitat. Successful invaders include species that can colonize disturbed areas, have rapid growth, reach maturity early, and reproduce prolifically. The most aggressive colonizers are often those with superior mechanisms for dispersal by human, wind, or animal vectors. Current rates of exotic species invasion seem rapid, $\sim$10 km $\cdot$ yr^{-1} (Mack

1986, Vitousek et al. 1996, Pitelka et al. 1997), but if considered on longer time scales, these rates would probably appear slower.

Invasions in the next 100 years will likely combine elements of short-term and long-term patterns and processes discussed above because both human actions and climate change are involved. Humans will be the primary agent of dispersal, and human-assisted migration may be a necessary conservation strategy for the survival of some native plant species. Climate will determine the potential limits for plants and animals, and current biogeographic barriers, like oceans and mountain ranges, may not be significant. The rapid rate of future climate change exceeds anything seen in the Holocene, and simple calculations suggest that native species will have to move or disperse at rates 40–50× faster than those observed in the paleoecologic record if they are to maintain equilbrium with the climate. It seems unlikely that most species will be able to do so, and disturbances, such as fire, may tip the balance in enabling their spread or extinction. Unfortunately, disturbance in the face of climate change will also create opportunities for non-native species to establish and flourish.

Although the past provides a key to the present and perhaps to the future, the past also highlights the unprecedented nature of the present and future. We have seen species in the past adapt to the magnitude of climate change projected in the next century but not at the projected rate (Overpeck et al. 1991). It is not clear that native species will be able to move across highly fragmented landscapes fast enough to survive, and management strategies will have to consider what level of intervention is acceptable. The projected ecological disruption also paves the way for exotic species invasions. Because future invasions stand as outliers to those witnessed in the past and present, managers and conservationists need to consider climate change explicitly in their planning efforts. As Hobbs and Huenneke (1992:333) observed:

> Nearly all systems are likely to be nonequilibrial in the future; we must be activists in determining which species to encourage and which to discourage. We cannot just manage passively, or for maximal diversity, but must be selective and tailor management to specific goals.

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NEW APPROACHES FOR SAMPLING AND MODELING NATIVE AND EXOTIC PLANT SPECIES RICHNESS

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ABSTRACT.—We demonstrate new multi-phase, multi-scale approaches for sampling and modeling native and exotic plant species to predict the spread of invasive species and aid in control efforts. Our test site is a 54,000-ha portion of Rocky Mountain National Park, Colorado, USA. This work is based on previous research wherein we developed vegetation sampling techniques to identify hot spots of diversity, important rare habitats, and locations of invasive plant species. Here we demonstrate statistical modeling tools to rapidly assess current patterns of native and exotic plant species to determine which habitats are most vulnerable to invasion by exotic species. We use stepwise multiple regression and modified residual kriging to estimate numbers of native species and exotic species, as well as probability of observing an exotic species in 30 × 30-m cells. Final models accounted for 62% of the variability observed in number of native species, 51% of the variability observed in number of exotic species, and 47% of the variability associated with observing an exotic species. Important independent variables used in developing the models include geographical location, elevation, slope, aspect, and Landsat TM bands 1–7. These models can direct resource managers to areas in need of further inventory, monitoring, and exotic species control efforts.

Key words: multi-scale sampling, multi-phase sampling, exotic invasive species, predictive spatial modeling, integrated approaches to environmental assessments, kriging.

Previous research suggests that habitats with high native plant species diversity can be more vulnerable to exotic plant species invasions than less species-rich areas (Stohlgren et al. 1998b, 1999a). To efficiently address threats posed by exotic species to native biodiversity, exotic plant species must be detected early. However, once an invasion has occurred, those populations and surrounding areas must be monitored to provide resource managers with the information needed to contain and control the exotic species.

Because only a small portion of any landscape can be affordably measured (usually $<1\%$), predicting species occurrences or other features over the remainder of the landscape requires accurate multi-scale techniques (Stohlgren et al. 1997d). Most native and exotic plant species, rare habitats, and hot spots of diversity are patchy on most landscapes, and so they are usually missed by single-phase, single-scale transects and small plots (Stohlgren et al. 1998a). In addition, many inventory and monitoring attempts are hampered by unknown sources and amounts of error. For example, inventories based on resource maps must include an assessment of what information would be gained by using a map of higher resolution (smaller minimum mapping unit; Stohlgren et al. 1997b), since many coarse-scale maps fail to recognize rare but important habitats.

This paper describes a sampling and spatial modeling approach that can provide resource managers with a clearer picture of which areas and habitats are vulnerable to invasion by exotic plant species. This information can improve resource management decisions for control of exotic species as well as the inventory and monitoring of native and exotic plant species.

A Multi-species, Multi-scale, Multi-phase Approach

The importance of conserving biological diversity is recognized worldwide, and recognition of the benefits of conserving biodiversity at the ecosystem level, rather than the individual species level (Noss 1983, Agee and Johnson 1988, LaRoe 1993), has resulted in the need to identify areas for protection based on their biodiversity. Stohlgren et al. (1997d) outlined an approach to a landscape-scale

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assessment of plant diversity to complement the National GAP Analysis Program (Scott et al. 1993). The approach recognizes that the resolution of investigation is the 1st source of potential error in identifying important habitats for conservation. Common minimum mapping units (MMUs) of 100 ha, 50 ha, and 2 ha failed to identify rare but important habitats such as aspen stands in the Beaver Meadows area of Rocky Mountain National Park, Colorado (Stohlgren et al. 1997b). Aspen stands are a keystone habitat in this area with unique and rich assemblages of plants (Stohlgren et al. 1997c), birds (T. Mabee personal communication), and butterflies (Simonson 1998). Thus, a key feature of our approach is to sample rare and common habitats with a stratified random sampling design. Unbiased vegetation sampling sites are selected in each stratum (Stohlgren et al. 1997b).

A 2nd source of error in assessing patterns of biodiversity results from single-scale sampling techniques. A comparison of several common sampling techniques demonstrated that small, single-scale plot and linear transect techniques missed many locally rare species, both native and exotic (Stohlgren et al. 1998a). In addition, valid extrapolations to larger areas were impossible. The Modified-Whittaker nested vegetation sampling plot consists of a 20 × 50-m plot that contains ten 1-m^2 subplots (6 systematically arranged around the inside of the plot perimeter and 4 systematically arranged around the outside of the 100-m^2 subplot perimeter), two 10-m^2 subplots (in diagonally opposite corners of the plot), and one 100-m^2 subplot (in plot center; Stohlgren et al. 1995, 1998a). The multi-scale data allow one to estimate the number of species found in an area larger than the area sampled (Stohlgren et al. 1997c).

Stohlgren et al. (1997c) tested a rapid biodiversity assessment using multi-phase, multi-scale sampling in the Beaver Meadows area mentioned above. Multi-phase sampling refers to using ground-truth plots (Modified-Whittaker), aerial photos, and satellite images to sample a specific characteristic, such as vegetation cover, at overlapping locations (Kalkhan et al. 1995). These multiple layers of data allow assessment of the accuracy of satellite image vegetation classification, and classifications can be improved from multiple layers of data (Kalkhan et al. 1998). The multi-scale Modified-Whittaker vegetation plot sampling design allowed identification of hot spots of biodiversity and a reasonable estimate of the total number of plant species expected to be found in the study area.

Data Comparability, Analysis, and Synthesis

In addition to identifying where species of interest and hot spots of diversity occur, multiple threats to native species diversity must be recognized so that appropriate management strategies can be developed. Using comparable sampling methods allows both local and regional analyses and monitoring of species diversity, for example, across management units. Sampling designs and methods must be able to accurately assess the effects of a particular management action or potential resource threat.

For example, data collected using the Modified-Whittaker plot have proven valuable for assessing impacts and outcomes. A grazing study in Rocky Mountain grasslands demonstrated that vegetation composition differences inside and outside grazing exclosures could not be attributed to the effects of grazing alone because of landscape heterogeneity in vegetation distributions that had not been sampled in earlier studies (Stohlgren et al. 1999b). Vegetation sampling in the U.S. central grasslands and Rocky Mountains showed that exotic plant species are invading areas with highest native plant species richness and cover (Stohlgren et al. 1998b, 1999a). Modified-Whittaker plots arranged along transects that cross forest ecotones in Rocky Mountain National Park, Colorado, provided information on understory species richness and species distributions (Stohlgren et al. 2000) and may provide a means to monitor changes in regional climate (Stohlgren et al. 1998c).

In recognition of the strengths of multi-scale sampling, the U.S. Forest Service Forest Health Monitoring Program has modified its single-scale understory vegetation sampling method so that it is comparable to the multi-scale Modified-Whittaker plot (Busing et al. 1999). Grand Staircase–Escalante National Monument, Utah, is using the multi-phase, multi-scale approach to inventory its vascular plant diversity and soil crust development (Stohlgren et al. 1997a). The Smithsonian Institution's Biodiversity Program has adopted the Modified-Whittaker vegetation sampling

TABLE 1. Summary statistics of data used in modeling species richness (native and exotic) and presence of exotic species in a 54,000-ha area of Rocky Mountain National Park, Colorado.

Variable	Minimum	Maximum	Mean	Standard deviation
Number native	0	27	7.20	4.7
Number exotic	0	6	0.59	1.0
Elevation (m)	2443	3639	2778	271.8
Slope (%)	0	33.36	13.62	8.5
Aspect	0	181	97.5	54.7
Band 1	47	92	60.5	9.1
Band 2	18	41	26.2	5.7
Band 3	15	54	26.9	9.0
Band 4	37	115	60.7	15.6
Band 5	30	156	71.5	27.8
Band 6	124	202	154.6	17.3
Band 7	11	90	33.6	17.0

design and successfully used the methods in Peru's Amazon basin (Stohlgren and Chong 1997). Many other federal and non-federal resource managers are adopting multi-scale approaches to inventory and monitor biodiversity.

Predictive models developed from multi-scale data are an excellent example of data synthesis for resource management (Kalkhan et al. 2000). Modeling small-scale variability in landscape characteristics requires the generation of full-coverage maps depicting characteristics measured at points in the field (Reich and Bravo 1998). While many spatial data sets describing land characteristics have proven reliable for macro-scale ecological monitoring, these relatively coarse-scale data fall short in providing the precision required by more refined ecosystem resource models (Gown et al. 1994). Spatial statistics and geostatistics provide a means of developing spatial models that can be used to correlate coarse-scale geographical data with multi-scale field measurements of biotic and abiotic variables (Kalkhan and Stohlgren 2000).

In summary, we have developed an inventory and monitoring approach where the resulting data are useful for many different applications at various scales. In the remaining portion of the paper, we introduce some preliminary results from our spatial modeling approach as an example of data analysis and synthesis.

METHODS

Field Data

To demonstrate the model procedures discussed in this paper, we used Modified-Whittaker vegetation data (ninety-four 1000-m^2 plots) from a 54,000-ha portion of Rocky Mountain National Park, Colorado, USA. Sample points were located based on stratified random sampling in vegetation cover types ranging from wet meadow to alpine tundra (procedure described in Stohlgren et al. 1997c). This data set is used to develop preliminary spatial models to predict species richness (native and exotic) and presence/absence of exotic species in 30 × 30-m cells.

GIS Data

The GIS database used to develop the models contained several coverages of independent variables thought to influence variability in species richness and the presence of exotic species. These included a 30-m-resolution Digital Elevation Model (DEM; Department of Interior, U.S. Geological Survey), which was used to create a 30-m grid overlay of percent slope and aspect (GRID, ARC/INFO; ESRI 1997). The database also included 30-m-resolution overlays of Landsat TM bands 1 through 7. The point coverage of the sample data was used to extract point estimates of elevation, slope, aspect, and the digital numbers associated with the 7 Landsat bands (Table 1).

Geostatistical Analysis

Multiple regression analysis was first used to explore variation in species richness and presence/absence of exotic species as a function of geographical location, elevation, slope, aspect, and Landsat TM bands 1–7 (Fig. 1). Stepwise regression was used to identify the best linear combination of independent variables.

Residuals of the regression models were computed and used for modeling their semi-

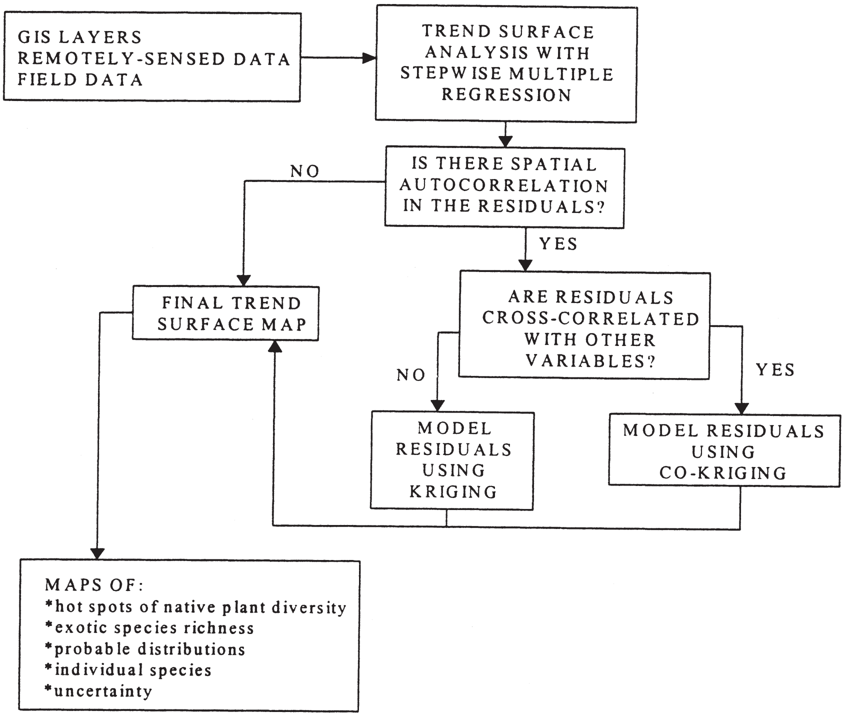

Fig. 1. Flow diagram of statistical procedures.

variograms. Model parameters were estimated using weighted least squares (Cressie 1985). We also analyzed residuals for spatial autocorrelation and cross-correlation (Czaplewski and Reich 1993, Reich et al. 1994, Bonham et al. 1995) with geographical variables. Inverse distance sampling was used to define the spatial weights matrix.

Estimates of the residuals were obtained using ordinary kriging. To obtain estimates of species richness (native and exotic) and presence of exotic species, we added regression estimates based on elevation, slope, aspect, etc., and estimated residuals computed using ordinary kriging. Kriging was carried out using the 4 nearest neighbors.

Modified residuals kriging models were cross-validated to assess variability in prediction errors. Cross-validation included deleting a single observation from the data set and predicting the deleted observation using remaining observations in the data set. We repeated this process for all observations in the data set. Summary statistics of estimated values were computed. Accuracies of the kriging models were assessed using the relative mean-squared error suggested by Havesi et al. (1992).

Spatial Integration

The ability to spatially model field data allows integration over any specified geographical region (i.e., point- and plot-level field data, management unit, watershed, region) to obtain a point estimate and associated standard error of prediction. This is accomplished by integrating the 3-dimensional response surface representing the variable of interest over the area of interest and dividing by the area. Since spatially modeled response surfaces can be represented as a grid in ARC/INFO (ESRI 1997), any specified region will contain a finite number (n) of grid cells of uniform size (i.e., 30 × 30 m). Our point estimate of a resource in some bounded region, A, is obtained by summing the point estimates associated with each cell, Φ_i, and dividing by the number of cells in the bounded region. It is also possible to obtain estimates of variance. Resource managers can use this information to determine which areas warrant further field data collection to increase model accuracy.

RESULTS

Regression Models

The regression model developed to describe variability in number of native species includes geographical location, elevation, and Landsat bands 1, 3, 5, 6, and 7 (Table 2). The positive correlation between elevation and number of native species suggests that species richness increases with increasing elevation. The number of native species was higher in northern and western portions of the study area. The significant Landsat TM bands provide information about differences in vegetation and soils throughout the study area and their influence on the richness of native and exotic species (Jensen 1996).

The regression model for number of exotic species includes geographical location, elevation, slope, aspect, and Landsat bands 2, 3, 5, 6, and 7 (Table 3). Exotic species were more prevalent in the southern and eastern portions of the study area and at lower elevations. The positive correlation with slope and the negative correlation with aspect indicate that exotic species are more prevalent on steeper, more northerly exposures. The positive correlation with number of native species indicates that exotic species are invading areas with high native plant species richness. This result agrees with the findings of Stohlgren et al. (1998b, 1999a) and Kalkhan and Stohlgren (2000).

The regression model to predict presence/absence of exotic species is similar to the one developed for number of exotic species (Table 4). The same factors that influence number of exotic species also influence probability of observing an exotic species.

The regression models accounted for 21% and 31% of variability observed in number of native and exotic species, respectively. The model developed to predict presence/absence of exotic species accounted for 38% of observed variability. Residuals of the regression models were positively spatially autocorrelated at the alpha = 0.05 level of significance. No significant cross-correlation was observed between residuals and independent variables used in developing the models. Residuals were approximately normally distributed.

TABLE 2. Regression model used to explain large-scale spatial variability of number of native species (in 30 × 30-m cell) in a 54,000-ha area of Rocky Mountain National Park, Colorado[a]. The x-, y-coordinates are in meters (UTM coordinates).

Variable	Coefficient	*P*-value
Intercept	–454.30	0.030
X-coordinate	–0.0002	0.0
Y-coordinate	0.0001	0.015
Band 1	0.3482	0.0
Band 3	–0.3936	0.0
Band 5	0.1072	0.0
Band 6	0.1452	0.0
Band 7	–0.1683	0.002
Elevation (m)	0.0058	0.0

[a] $R^2 = 0.208$, standard error = 4.22, n = 940 1-m² plots.

TABLE 3. Regression model used to describe large-scale spatial variability in number of exotic species (in 30 × 30-m cell) in a 54,000-ha area of Rocky Mountain National Park, Colorado[a]. The x-, y-coordinates are in meters (UTM coordinates).

Variable	Coefficient	*P*-value
Intercept	83.422	0.065
X-coordinate	0.00003	0.0
Y-coordinate	–0.00002	0.039
Band 2	–0.0966	0.0
Band 3	0.0560	0.007
Band 5	0.0386	0.0
Band 6	–0.0082	0.074
Band 7	–0.0528	0.0
Elevation (m)	–0.0011	0.0
Slope (%)	0.0069	0.081
Aspect	–0.0011	0.066
Number native	0.0803	0.0

[a] $R^2 = 0.314$, standard error = 0.839, n = 940 1-m² plots.

TABLE 4. Regression model used to describe large-scale spatial variability in probability of presence of exotic species (in 30 × 30-m cell) in a 54,000-ha area of Rocky Mountain National Park, Colorado[a]. The x-, y-coordinates are in meters (UTM coordinates).

Variable	Coefficient	*P*-value
Intercept	38.89	0.05
X-coordinate	0.000	0.001
Y-coordinate	–0.000	0.04
Band 2	–0.045	0.001
Band 3	0.029	0.001
Band 5	0.015	0.001
Band 7	–0.019	0.001
Elevation (m)	–0.001	0.001
Slope (%)	0.007	0.001
Aspect	–0.001	0.05
Number native	0.037	0.001

[a] $R^2 = 0.383$, standard error = 0.377, n = 940 1-m² plots.

TABLE 5. Parameter estimates of the semivariograms used to describe spatial continuity in the residuals.

Regression model	Nugget	Sill	Range	Semivariogram model
Native	15.94	1450	32704728	exponential
Exotic	0.763	1.117	151.4	Gaussian
Probably exotic	0.081	0.187	215.1	Gaussian

Kriging

Model parameter estimates of the semivariograms for the 3 models are given in Table 5. The large range associated with residuals for native species suggests the presence of large-scale spatial continuity in number of native species across the study area. In contrast, the small range associated with exotic species models indicates that exotic species occur in small patches throughout the study area. The large nugget effect relative to the sill for these 2 models also suggests a considerable variation within these patches.

The modified residual kriging model for number of native species had a relative mean-squared error of 8.39 ($R^2 = 0.625$), while, in comparison, the regression model had a relative mean-squared error of 17.81 ($R^2 = 0.208$; Table 6). Kriging the residuals reduced the relative mean-squared error by 53%. The modified residual kriging model for number of exotic species had a relative mean-squared error of 0.501 ($R^2 = 0.506$), which represents a reduction in relative mean-squared error of 29%. Similar mean-squared errors were observed for the probability model of exotic species. Larger errors associated with exotic species models are due primarily to the small-scale spatial heterogeneity associated with the occurrence and density of exotic species. This small-scale spatial heterogeneity makes it difficult to predict spatial variability in presence/absence or number of exotic species at the 1000-m^2 plot scale.

DISCUSSION

We have outlined a comprehensive approach to sampling and modeling native and exotic plant species for natural resources management. Our approach provides an alternative to individual-based reaction-diffusion and spatially explicit simulation models and their assumptions and limitations (see Higgins et al. 1996). For example, the use of full-coverage, fine-scale variables (e.g., Landsat TM data with a 30 × 30-m resolution) is a valuable addition to spatial modeling and addresses problems relating to lack of empirical data and inappropriate scales that affect previously mentioned types of models. Also, our approach is based on current species locations, and so no direct assumptions are made about dispersal or autecology (see Kot et al. 1996)

The multi-phase, multi-scale sampling and modeling methods are easily modified for application across management units and even biomes and taxonomic groups (e.g., birds and butterflies as well as plants). The sampling methods are efficient and accurate in the field, and the development of automated data management and analysis tools will facilitate data use for local management as well as basic research and synthesis.

Data collected for a rapid assessment of plant diversity patterns were immediately useful for modeling native and exotic plant distributions across the landscape (Kalkhan and Stohlgren 2000). This information could be used by resource managers to set priorities and quickly target hot spots of exotic plant diversity for control efforts. Alternatively, or simultaneously, they might target areas of recent invasion where control efforts are relatively less expensive. Likewise, corridors of invasion, such as roads and riparian zones, might be targeted for control (Greenberg et al. 1997, Stohlgren et al. 1998b).

Additional variables, such as soil characteristics, will enhance the models' predictive capabilities (Kalkhan and Stohlgren 2000). The combination of spatial statistics and stepwise multiple regressions greatly increased the predictive capabilities of our models for estimating the numbers of native and exotic species and the probability of encountering an exotic species. One of the strengths of this modeling approach is the ability to develop maps of "uncertainty" based on subsampling the data with Monte-Carlo simulations (Kalkhan et al.

TABLE 6. Relative mean-squared errors associated with estimating number of native and exotic species and probability of observing an exotic species in a 30 × 30-m cell.

Regression model	Estimation technique	Relative mean-squared error	R^2
Native	Regression	17.81	0.208
	Kriging	8.39	0.625
Exotic	Regression	0.704	0.314
	Kriging	0.501	0.506
Probably exotic	Regression	0.142	0.383
	Kriging	0.121	0.470

2000). This provides land managers with a spatial representation of the confidence of the model and completeness of plot data. The multi-phase sampling approach (i.e., data from ground-truth plots, air photos, and Landsat TM images) provides additional ways to assess vegetation classification accuracy and determine where more ground-truth plots are needed (Kalkhan et al. 1998).

Similar models can be developed for individual species in more restricted areas (with a greater density of sample points) to better understand their ecology (where they are able to occur) and patterns of spread. We are developing spatial models for many common invasive plant species in Rocky Mountain National Park to better understand the effects of grazing, natural and prescribed fire, and rapid climate change on invasive plant species.

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ANNOTATED CHECKLIST OF EXOTIC VASCULAR PLANTS IN YELLOWSTONE NATIONAL PARK

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ABSTRACT.—Documentation of the arrival of exotic vascular plants in Yellowstone National Park has been sporadic. An annotated checklist of exotic vascular plants is presented, with information about the approximate arrival time in the park of each species and the current extent of the infestation. Yellowstone's flora includes 187 exotic vascular plant species (14.8% of the flora), and the park has an extrapolated mean number of exotic species per 10 km^2 of 47.3. The situation in Yellowstone is compared with other areas in North America. The increase in exotics mirrors a corresponding increase in visitation.

Key words: Yellowstone National Park, exotic plants, flora, vascular plants, annotated checklist.

The intense interest generated by the expeditions of Folsom and Cook in 1869 and Langford, Washburn, and Doane in 1870 led to the establishment of Yellowstone as the 1st national park in the world in 1872. The 1st botanical collection was by Robert Adams, Jr., who was a member of the 1871 Hayden expedition. The earliest known record of an exotic species in Yellowstone is *Oxalis violacea* Jacq., which was collected by Forwood in 1881 (Denton 1973). The 1st Yellowstone flora was published by Frank Tweedy (1886), who incorporated the work of several collectors and listed 657 species, including 6 species that, if correctly identified, are exotic. Thus, a relatively early baseline of information exists that predates most major disturbance by visitors. In 1900, Per Axel Rydberg completed a catalogue of the vascular plants of Montana and Yellowstone National Park and reported 8 species that appear to be exotic, including 4 that were reported by Tweedy. These early floras did not include all collections that had been made within Yellowstone, omitting, for example, the Forwood collection of *Oxalis violacea.* Intense interest in the park resulted in many other collectors visiting and making extensive collections that are now scattered among many different institutions. Examination of material at Yellowstone National Park (YELLO), Montana State University (MONT), and Rocky Mountain Herbarium (RM) resulted in the location of specimens documenting the presence of at least 12 exotic species in the park by 1900. Other collections, such as many of those cited by Tweedy and Rydberg, are at East Coast herbariums such as the New York Botanical Gardens (NY) and the Smithsonian Institution (US) and therefore were not easily available for examination.

A significant interval has passed since the last flora was published for Yellowstone National Park (Despain 1975). In the intervening time exotics have continued to arrive and spread in Yellowstone. The purpose of this paper is to provide an updated annotated checklist of exotics known to occur within the park.

Precise demarcation of exotic species can be difficult. A species is considered exotic by the National Park Service if it occurs in a given place as a result of direct or indirect, deliberate, or accidental actions by humans (NPS 1988). Species that are native to North America, but would not be found within the confines of the park without human intervention, are therefore considered exotic.

During the early years of the park, several species including *Syringa vulgaris* L., *Picea pungens* Engelm., and *Populus* spp. were intentionally planted in Mammoth and at other locations in the park. The annotated checklist of exotic plants does not include any species that was intentionally planted if the original plant has not reproduced or spread from the historical planting. Because one goal of the National Park Service is to prevent the establishment of exotic species, any new arrival is

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eradicated if possible. Therefore, some species that might not persist and reproduce within the confines of the park are included in this list.

The origins of several cosmopolitan weeds that occur in Yellowstone, such as *Amaranthus retroflexus* L., *Poa pratensis* L., *Polygonum aviculare* L., and *Rorippa nasturtium-aquaticum* (L.) Hayek, have spawned intense debate in the literature and may never be satisfactorily resolved (Cronquist et al. 1977, Stuckey and Barkley 1993, Rejmánek and Randall 1994). The decision to include *Amaranthus retroflexus, Poa pratensis, Polygonum aviculare,* and *Rorippa nasturtium-aquaticum* as exotic species to Yellowstone is somewhat arbitrary, yet generally consistent with records of the earliest collections in the park.

Documentation of the arrival of exotics has been somewhat sporadic through the years. The first 50 years after the park's establishment was a time of intense collecting, but interest in and documentation of exotics varied from collector to collector. P.H. Hawkins and H.S. Conard in the 1920s collected extensively in the park and documented many exotics for the 1st time. Interest in documenting exotic species presence in the park then dwindled until the early 1950s, when Ray Davis documented the presence of an additional 28 species. The arrival of plant ecologist Don Despain in Yellowstone in 1972 renewed interest in the flora of the park and resulted in publication of a flora reporting 86 exotics (Despain 1975). Additional new records of exotics were documented during habitat mapping of the entire park during the late 1970s. Yellowstone's Exotic Vegetation Management Plan (NPS 1986) listed 89 species of exotics but failed to mention several species reported in Despain (1975). The intensification of interest and alarm about the spread of exotics has resulted in a determined effort by the National Park Service to document all exotics present in the park and eradicate new arrivals, if possible, before they become established (Olliff et al. 2001). Currently, 187 species of exotics (188 taxa) are known to occur or have occurred in the past within the confines of the park, and new taxa are located almost every year.

Even though visitors come from all over the world to visit Yellowstone, origins of the exotic species do not reflect this wide diversity. The primary source of exotics is Eurasia, representing 93.6% of the exotic flora, as is typical in many parts of the United States (Rejmánek and Randall 1994, Sheley et al. 1999). The remainder are from North America (5.3%) and Central and South America (1.1%).

Because the incidence and spread of exotics is escalating, more interest is focused on the magnitude of the problem. Several methods have been used to present information about the presence of exotics in a flora. The total number of exotic taxa, of interest in itself, provides no way to compare diverse areas, especially when the areas to be contrasted are of significantly different size. Another commonly used comparison is the percentage of the flora that is exotic. This method has some of the same problems as the number of exotic species. In addition, the percentage can be highly influenced by the relative diversity of the flora, allowing comparable-sized areas with the same number of exotics to have very different percentages. Rejmánek and Randall (1994) used the number of species $\cdot$ log(area)$^{-1}$ as a standardized expression of exotic species richness. When used with log to the base 10, this index corresponds to the extrapolated mean number of exotic species $\cdot$ 10 km^{-2}. The high number of exotics centered near developed areas, roads, and trails in Yellowstone skews this result. The likelihood of finding a particular 10-km^2 plot with this exact number of exotics is low. Even with these difficulties, this method allows comparison among areas of greatly different sizes and native flora richness (Table 1). The infestation of exotics is greater than might be expected in Yellowstone, given that most of the park is de facto wilderness and has not been logged, farmed, or grazed by domestic stock.

Most exotic vascular plants currently known from within Yellowstone National Park are also widespread in adjacent states. Yellowstone, though, is a destination for visitors from throughout the United States and the world. The 1st report of an exotic for the state of Wyoming has not infrequently been from Yellowstone National Park. The annotated checklist includes 11 species not reported by the most recent flora of Wyoming (Dorn 1992): *Centaurea* × *pratensis, Cerastium glomeratum, Hieracium caespitosum, H. flagellare, H. floribundum, Holosteum umbellatum, Prunus avium, Senecio jacobaea, Trifolium aureum, T. campestre, Vicia cracca.*

The escalating number of exotics mirrors the steadily increasing visitation to the park

TABLE 1. Species richness of exotic vascular plant floras at selected locations in the United States.

Region	Number of native species	Number of exotic species	Percentage of exotic species	Number of exotic species per log(area)
Alaska[1]	1229	144	10.5	23.3
California[1]	4844	1025	17.5	182.6
Glacier N. P.[2]	1131	126	11.1	34.9
Great Plains[1]	2495	394	13.6	63.5
Great Smoky Mountains N. P.[3]	1573	341	21.7	102.6
New York[1]	1940	1082	35.8	210.5
Utah[1]	2572	444	14.7	83.1
Western Montana[1]	1251	250	16.7	64.2
Wyoming[4]	2761*	348*	12.6	64.4
Yellowstone N. P.	1265	187	14.8	47.3
Yosemite N. P.[5]	1352	126	9.3	36.2

[1] Modified from Rejmánek and Randall 1994
[2] Peter Lesica personal communication
[3] Janet Rock personal communication
[4] Fertig 1999
[5] Jan VanWagtendonk personal communication
* = total number of taxa (not species)

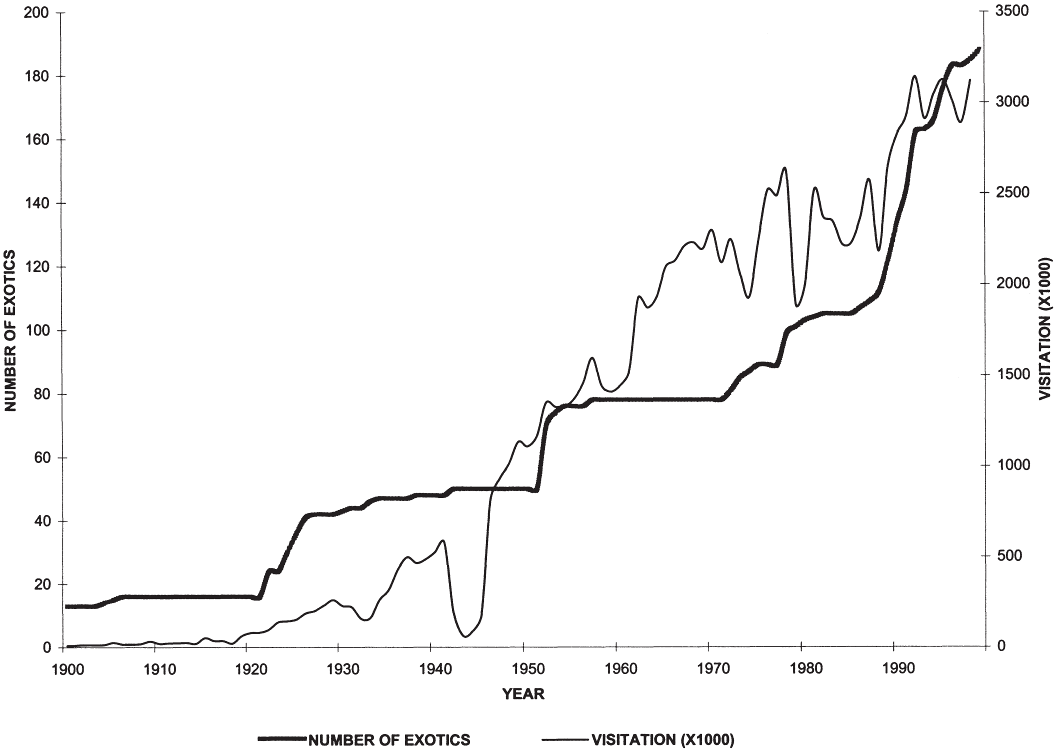

Fig. 1. Number of exotic plant taxa occurring in Yellowstone National Park based on herbarium records compared with visitation to the park based on official records since 1900.

(Fig. 1). The correlation between increasing visitation and increasing numbers of exotics has been noted previously in other national park units (Lesica et al. 1993). The arrival of new exotic plants into Yellowstone associated with vehicles, muddy shoes, equipment, and stock is likely to persist unabated. Continued vigilance is needed to eradicate new exotic species to the park prior to their becoming established.

The annotated checklist represents the current state of knowledge about the exotic flora

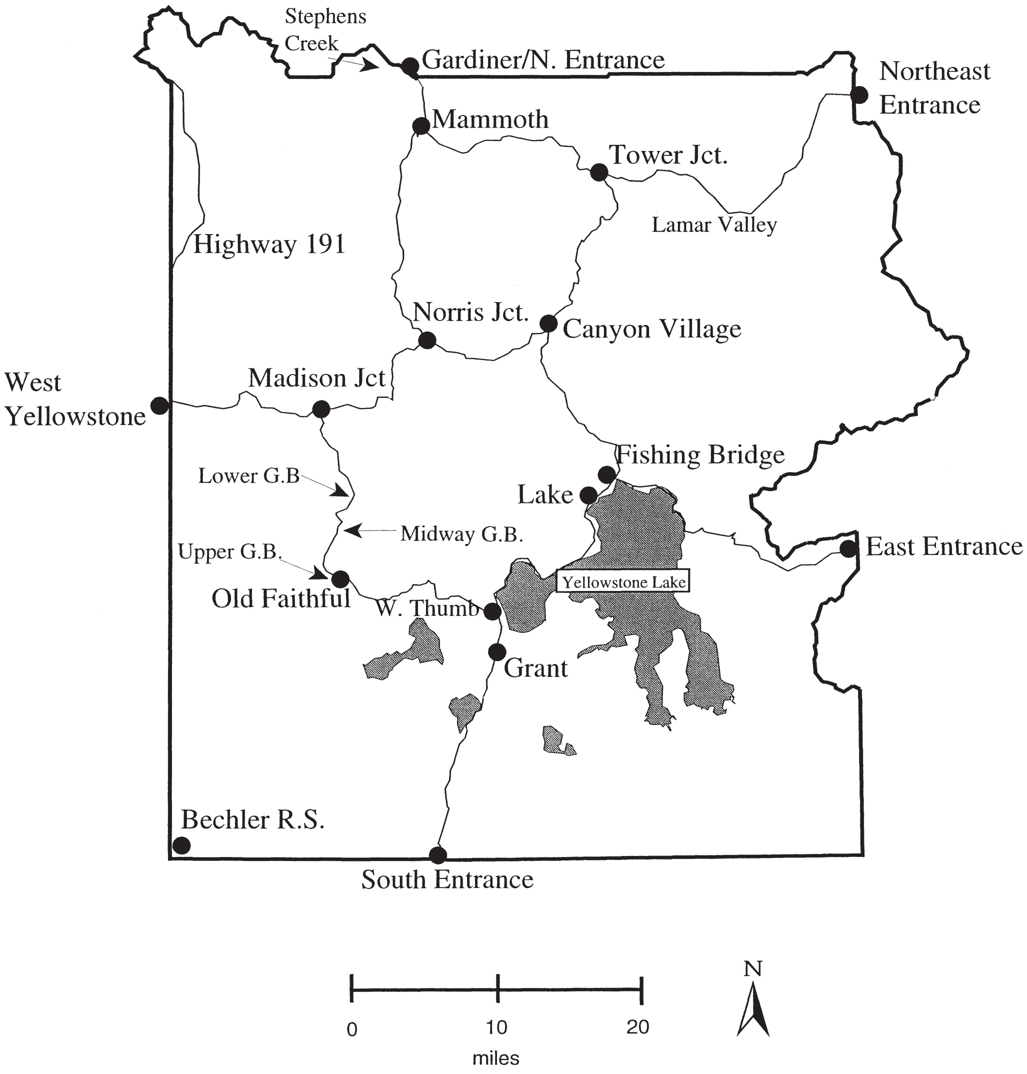

Fig.2. Map of Yellowstone National Park.

of Yellowstone and is based primarily on a review of specimens at the Yellowstone National Park herbarium. The Montana State University herbarium and Rocky Mountain Herbarium were also consulted, resulting in documentation of a minimum of 12 exotic species in the park by the turn of the 20th century. The review of specimens was not exhaustive; additional material that was not examined may be present at these facilities. The extensive early and continual interest in Yellowstone National Park has resulted in collections of Yellowstone material now housed throughout the country. As these collections are examined and additional literature citations located, the time of establishment of many exotic species will be further refined. Regretfully, the timing of arrival of many species will never be known exactly, due to the sporadic collecting efforts that focused on exotic species.

The annotated list is arranged alphabetically by family, genus, and species. Nomenclature follows Dorn (1992) except that traditional names for families were used as in Hitchcock and Cronquist (1973). Following the scientific name, common names are provided as used in Yellowstone or adjacent states (Hitchcock and Cronquist 1973, Whitson et al. 1992, Welsh et al. 1993, Stubbendieck et al. 1995). The earliest herbarium record that could be located is cited by herbarium code and year of collection. In some cases information exists in records that suggests an earlier arrival time; due to an inability to verify these reports, this information was not included in the graph of arrival times (Fig. 1). Noxious species as listed by the states of Idaho, Montana, and Wyoming are noted. A brief summation of the current status of the species in the park completes the information provided. Information about the location and extent of various species was augmented by the author's personal observations. A map of Yellowstone, including reference to areas commonly mentioned in the annotated list, is also provided (Fig. 2). Exotic species that had been reported previously, but which were based on misidentified material or for which no specimens could be located, include the following: *Artemisia vulgaris* L., *Callitriche anceps* Fern., *Chenopodium album* L., *Foeniculum vulgare* Mill., *Silene noctiflora* L., and *Spergularia marina* (L.) Griseb.

ANNOTATED LIST OF EXOTIC PLANTS OF YELLOWSTONE NATIONAL PARK

ACERACEAE

Acer negundo L.; box-elder; YELLO (1979); 2 roadside shrubs in the Mammoth area (highly browsed, not able to discern variety)

AGAVACEAE

Yucca glauca Nutt.; Great Plains yucca, soapwell; YELLO (1996); a few plants at 1 campsite at Mammoth campground, not persisting

AMARANTHACEAE

Amaranthus retroflexus L.; redroot pigweed, rough pigweed; YELLO, 1952; disturbed areas around Mammoth, Gardiner, and Stephens Creek

BORAGINACEAE

Amsinckia menziesii (Lehm.) Nels. & Macbr.; Menzies' fiddleneck; YELLO (1991); disturbed ground at the South Entrance

Asperugo procumbens L.; catchweed, madwort; YELLO (1979); around Mammoth, Stephens Creek, and Gardiner

Cynoglossum officinale L.; houndstongue; YELLO (1953); listed noxious by MT, WY; infestation around Mammoth and near the East Entrance

Lappula squarrosa (Retz.) Dum. var. *squarrosa*; European stickseed, European sticktight; YELLO (1989); scattered occasionally along roadsides

Lithospermum arvense L.; corn gromwell; YELLO (1989); Mammoth and Gardiner

Myosotis micrantha Pallas ex Lehm.; blue scorpion-grass, small-flower forget-me-not; YELLO (1990); Upper Geyser Basin and West Thumb Geyser Basin

CAMPANULACEAE

Campanula rapunculoides L.; creeping bellflower, rover bellflower; YELLO (1992); apparently planted historically around residences on Officer's Row in Mammoth and persisting in lawns and along building edges

CANNABACEAE

Cannabis sativa L.; marijuana, hemp; YELLO (1995); located and eradicated at least twice along roadside of Highway 191

Humulus lupulus L. var. *neomexicanus* Nels. & Cock.; hops; YELLO (1978); perhaps planted historically, a few plants persisting around Mammoth and Grant Village near buildings

CAPRIFOLIACEAE

Lonicera tatarica L.; Tatarian honeysuckle; YELLO (1988); planted historically around Mammoth and occasionally spreading into adjacent sinkholes

CARYOPHYLLACEAE

Arenaria serpyllifolia L.; thyme-leaf sandwort; YELLO (1989); a few locations in Upper and Lower geyser basins

Cerastium glomeratum Thuill.; sticky chickweed; YELLO (1995); spreading in Midway and Lower geyser basins

Cerastium fontanum Baumg.; mouse-ear chickweed; YELLO (1926); Upper and Lower geyser basins, Mammoth, and other scattered sites around park

Dianthus armeria L.; grass pink; RM (1981), YELLO; near Old Faithful, Midway Geyser Basin, and on the West Entrance road

Dianthus barbatus L.; sweet william; YELLO (1992); roadside near Blacktail Drive possibly intentionally spread from seed packet, eradicated

Gypsophila paniculata L.; baby's breath; YELLO (1978); perhaps planted historically, occasional plants along roadsides near Mammoth

Holosteum umbellatum L.; jagged chickweed, holosteum; YELLO (1992); Mammoth Terraces

Saponaria officinalis L.; bouncing-bet, soapwort; YELLO (1952); perhaps planted historically, occasional near houses around Mammoth

Silene latifolia Poir.; white campion, white cockle; YELLO (1924); disturbed ground along roadsides and in developed areas

Silene vulgaris (Moench) Garcke; bladder campion; YELLO (1990); roadsides and spreading, especially along the Northeast Entrance road

Spergularia rubra (L.) J. & K. Presl; red sandspurry; MONT (1922), YELLO; widespread and naturalized

Stellaria media (L.) Vill.; common chickweed; YELLO (1992); scattered locations including Mammoth

Vaccaria hispanica (Miller) Rauschert; cowcockle, cowherb; RM (1899); disturbed areas historically by Gardner River, not located recently in park

CHENOPODIACEAE

Atriplex heterosperma Bunge; two-seed orache; YELLO (1996); 1 site near Rattlesnake Butte

Atriplex hortensis L.; garden orache, sea purslane; YELLO (1952); label states Gardiner dumps, not recently located within park

Atriplex rosea L.; red orache, tumbling orache; YELLO (1952); on disturbed ground near Stephens Creek

Bassia hyssopifolia (Pallas) Kuntze; bassia, five-hook bassia; YELLO (1995); Yellowstone River Trail near Gardiner

Kochia scoparia (L.) Schrad.; summer cypress, kochia; YELLO (1957); widespread on disturbed soil near Gardiner

Salsola australis R. Br.; Russian thistle, tumbleweed; YELLO (1926); widespread on disturbed ground near Gardiner and Mammoth

Salsola collina Pallas; Pallas' tumbleweed; YELLO (1990); along roadsides near Gardiner and Mammoth

COMPOSITAE

Anthemis tinctoria L.; yellow chamomile; YELLO (1992); 1 plant eradicated in parking lot of Administration Building at Mammoth

Arctium sp. (Hill) Bernh.; burdock; YELLO (1999); *Arctium minus* Bernh. listed noxious by WY; 1 vegetative plant eradicated in lawn at Mammoth, probably *Arctium minus*

Artemisia absinthium L.; wormwood, absinthium; YELLO (1992); isolated plants along roads, apparently not reproducing

Carduus acanthoides L.; plumeless thistle, acanthus thistle; YELLO (1992); listed noxious by WY; 1 infestation near Tuff Cliff north of Madison Junction

Carduus nutans L.; musk thistle, nodding thistle; YELLO (1973); listed noxious by ID, WY; a few small infestations scattered throughout park

Centaurea diffusa Lam.; diffuse knapweed; YELLO (1989); listed noxious by ID, MT, WY; occasional plants along roadsides

Centaurea maculosa Lam.; spotted knapweed; YELLO (1973); listed noxious by ID, MT. WY; established in scattered areas such as around Mammoth, Fountain Paint Pots, and along the West Entrance Road

Centaurea × *pratensis* Thuill.; meadow knapweed; YELLO (1990); listed noxious by ID; discovered as only 1 plant and eradicated

Centaurea repens L.; Russian knapweed; YELLO (1989); listed noxious by ID, MT, WY; a few small infestations near North Entrance and Reese Creek

Chrysanthemum leucanthemum L.; oxeye daisy; YELLO (1927); listed noxious by MT, WY (as *Leucanthemum vulgare* Lam.); infestations at Mammoth and Madison Junction

Cichorium intybus L.; chicory, wild succory, bluesailors; YELLO (1990); occasional single plants found along road edge and eradicated

Cirsium arvense (L.) Scop. var. *horridum* Wimm. & Grab.; Canada thistle, creeping thistle; YELLO (1934); listed noxious by ID, MT, WY; widespread throughout park including backcountry

Cirsium vulgare (Savi) Tenore; bull thistle, common thistle; YELLO (1952); several infestations along roads, in developed areas, and in backcountry

Crepis tectorum L.; annual hawksbeard; YELLO (1953); established in southern portion of park and at several other locations

Filago arvensis (L.) L.; field filago; YELLO (1992); spreading at several locations

Hieracium aurantiacum L.; orange hawkweed, orange king devil; YELLO (1978); listed noxious by ID, MT; roadside infestations at several locations

Hieracium caespitosum Dumort.; yellow hawkweed, yellow king devil; MONT (1992), YELLO; listed noxious by ID, MT; roadside infestations at several locations

Hieracium flagellare Willd.; whiplash hawkweed; YELLO (1996); established along roadside near Sand Point

Hieracium floribundum Wimmer & Grab.; glaucous king devil; YELLO (1994); listed noxious by MT; established along roadside near Tuff Cliff

Lactuca serriola L.; prickly lettuce; YELLO (1952); widespread on disturbed soil near roads

Matricaria maritima L.; scentless may weed, scentless chamomile; YELLO (1987); occasional along roadsides

Onopordum acanthium L.; scotch thistle, cotton thistle, winged thistle; YELLO (1991); listed noxious by ID, WY; at least 2 separate establishments of single plants that were eradicated

Ratibida columnifera (Nutt.) Wooton & Standley; prairie coneflower; MONT (1900), YELLO; occasional plant along roadside, not persisting

Sececio jacobaea L.; tansy ragwort; YELLO (1990); listed noxious by ID, MT; 1 plant eradicated from roadside in Lower Geyser Basin

Senecio vulgaris L.; common groundsel; YELLO (1992); Fern Cascades trail at Old Faithful

Solidago rigida L. var. *humilis* Porter; stiff goldenrod; YELLO (1998); 1 roadside plant eradicated near Antelope Creek

Sonchus arvensis L.; perennial sow-thistle, field sow-thistle; YELLO (1989); listed noxious by WY, ID; spreading from several infestations

Sonchus asper (L.) Hill; prickly sow-thistle, spiny sow-thistle; YELLO (1933); occasionally scattered around park

Sonchus uliginosus Bieb.; marsh sow-thistle, meadow sow-thistle; YELLO (1978); spreading from several infestations

Tanacetum vulgare L.; common tansy; YELLO (1973); listed noxious by MT; a few scattered plants along roadsides

Taraxacum laevigatum (Willd.) DC.; red-seeded dandelion; YELLO (1926); naturalized parkwide

Taraxacum officinale Weber; common dandelion; YELLO (1924); naturalized parkwide

Tragopogon dubius Scop.; yellow salsify, western salsify; MONT (1922), YELLO; widespread

Tragopogon porrifolius L.; salsify, vegetable oyster, oyster plant; YELLO (1925); Stephens Creek, not recently relocated

Tragopogon pratensis L.; meadow salsify, Jack-go-to-bed-at-noon; YELLO (1925); scattered along roadsides, especially on northern range

CONVOLVULACEAE

Convolvulus arvensis L.; field bindweed, field morning-glory; YELLO (1952); listed noxious by ID, MT, WY; established along roads primarily near Mammoth, Gardiner, and along Highway 191

CRUCIFERAE

Alyssum alyssoides (L.) L.; pale alyssum, yellow alyssum; YELLO (1952); scattered locations in park including all over Mammoth Terraces

Alyssum desertorum Stapf; desert alyssum, dwarf alyssum; YELLO (1972); abundant in undisturbed vegetation near Gardiner and Stephens Creek

Barbarea vulgaris R. Br.; bitter wintercress, yellow rocket; YELLO (1924); occasional plants along roadsides and developed areas

Berteroa incana (L.) DC.; berteroa, hoary allysum; YELLO (1986); dense along roadside near West Entrance and at other scattered locations

Brassica kaber (DC.) Wheeler; wild mustard, charlock; YELLO (1954); disturbed area near Mammoth, not located recently in park

Brassica rapa L.; field mustard, rape, birdsrape mustard; RM (1899), YELLO; disturbed areas historically, not located recently in park

Camelina microcarpa Andrz. ex DC.; smallseed falseflax, littlepod falseflax; MONT (1922), YELLO; occasional, especially on northern range

Camelina sativa (L.) Crantz; false flax, gold-of-pleasure; RM (1899); near Undine Falls, not located recently in park although reported as "[v]ery abundant in some places on the roadside" (Nelson 1899)

Capsella bursa-pastoris (L.) Medic.; shepherd's purse; RM (1899), YELLO; widespread in thermal areas and disturbed places

Cardaria chalepensis (L.) Hand.-Mazz.; chalapa hoarycress, orbicular whitetop; YELLO (1995); listed noxious by MT (as *Cardaria* spp.), WY (as *Cardaria* spp.); near Gardiner

Cardaria draba (L.) Desv.; hoary cress, whitetop; YELLO (1995); listed noxious by ID, MT, WY; 1 infestation along northeast entrance road

Cardaria pubescens (Meyer) Jarmol.; hairy whitetop, globepodded hoarycress; YELLO (1931); listed noxious by MT (as *Cardaria* spp.), WY; established near Gardiner and Mammoth

Chorispora tenella (Pallas) DC.; blue mustard, musk mustard; YELLO (1996); small population along Coyote Creek trail near northern boundary

Descurainia sophia (L.) Webb ex Prantl; flixweed, bed-ground-weed; YELLO (1952); occasional sites, especially on northern range

Draba verna L.; whitlow-grass, spring draba; RM (1980), YELLO; spreading throughout Upper Geyser Basin

Hesperis matronalis L;. dame's rocket, damask violet, sweet rocket; YELLO (1978); perhaps planted historically, occasional plants persisting in vicinity of Mammoth

Isatis tinctoria L.; dyer's woad; YELLO (1992); listed noxious by ID, MT, WY; 4 separate establishments of single plants, eradicated

Lepidium campestre (L.) R. Br.; fieldcress, field pepperweed; YELLO (1992); occasional plants along roadsides

Lepidium perfoliatum L.; clasping peppergrass, clasping pepperweed; YELLO (1978); on disturbed ground at several locations in park

Lepidium sativum L.; garden cress; YELLO (1990); Mammoth along Officer's Row

Rorippa nasturtium-aquaticum (L.) Hayek; watercress; YELLO (1922); widespread especially in thermal areas

Sisymbrium altissimum L.; tumblemustard, Jim Hill mustard; MONT (1922), YELLO; common in disturbed areas along roads and near developed areas

Sisymbrium loeselii L.; Loesel tumblemustard, tallhedge mustard; YELLO (1975); occasional along roads and in developed areas

Thlaspi arvense L.; fanweed, field pennycress; RM (1906), YELLO; widespread on disturbed ground

CYPERACEAE

Scirpus atrocinctus Fern.; wool-grass; YELLO (1996); a few plants persisting in roadside ditch near Yellowstone Lake

DIPSACACEAE

Dipsacus fullonum L.; teasel; YELLO (1992); several plants eradicated from roadside

EUPHORBIACEAE

Euphorbia esula L. var. *uralensis* (Fisch. ex Link) Dorn; leafy spurge; YELLO (1991); listed noxious by ID, MT, WY; 1st written report in park in 1983, several small infestations scattered around park

Euphorbia maculata L.; spotted spurge; RM (1980), YELLO; West Thumb Geyser Basin

GERANIACEAE

Erodium cicutarium (L.) L'Her. ex Aiton; filaree, stork's-bill; YELLO (1974); established in several thermal areas including Mammoth Hot Springs and the Upper Geyser Basin

GRAMINEAE

Agropyron cristatum (L.) Gaertn. var. *desertorum* (Fisch. ex Link) Dorn; crested wheatgrass; YELLO (1942); deliberately planted in the Stephens Creek area in the northern portion of the park in the 1950s and occasionally spreading

Agropyron triticeum Gaertn.; annual wheatgrass; YELLO (1952); widespread in undisturbed areas near Gardiner

Agrostis stolonifera L.; red top, creeping bentgrass; YELLO (1924); widespread along roads

Aira caryophyllea L.; silver hairgrass; RM (1982), YELLO; known only from vicinity of Firehole Lake in Lower Geyser Basin

Alopecurus arundinaceus Poiret; creeping foxtail; YELLO (1990); a few scattered locations, especially along roads

Alopecurus pratensis L.; meadow foxtail; YELLO (1978); scattered locations including the backcountry

Apera interrupta (L.) Beauv.; Italian sandgrass, interrupted apera; YELLO (1991); Mammoth Terraces

Arrhenatherum elatius (L.) J. & K. Presl; tall oatgrass, tuber oatgrass; YELLO (1989); eradicated 3 times from roadside

Avena fatua L.; wild oats; YELLO (1990); roadside near Mammoth Terraces

Avena sativa L.; common oats; YELLO (1989); rarely present and not persisting along roadsides in the Gallatin and Stephens Creek area

Bromus briziformis Fisch. & Meyer; rattlesnake chess; YELLO (1925); historically in Mammoth area, currently along 1 area of Old Gardiner Road

Bromus inermis Leyss. var. *inermis*; smooth brome; YELLO (1925); widespread in northern range of park, especially in Lamar Valley and near roadsides

Bromus japonicus Thunb. ex Murray; Japanese brome; YELLO (1986); along roads in northern portion of park, especially near Gardiner and Stephens Creek

Bromus tectorum L.; cheatgrass, downy brome, downy chess; YELLO (1930); present and widely distributed in park, especially in thermal areas and northern range

Dactylis glomerata L.; orchard-grass; YELLO (1978); occasional along roadsides

Elymus hispidus (Opiz) Melderis var. *hispidus*; intermediate wheatgrass; YELLO (1999); a few patches scattered along roads

Elymus hispidus (Opiz) Melderis var. *ruthenicus* (Griseb.) Dorn; intermediate wheatgrass; YELLO (1990); a few patches scattered along roads and in developed areas

Elymus junceus Fisch.; Russian wild rye; YELLO (1988); apparently planted during 1960s and/or 1970s for revegetation and persisting

Elymus repens (L.) Gould; quackgrass, couchgrass; YELLO (1952); listed noxious by WY [as *Elytrigia repens* (L.) Nevski]; well established near Gardiner and at scattered locations along roads

Festuca arundinacea Schreb.; tall fescue; YELLO (1995); 1 site near Old Gardiner Road

Festuca pratensis Huds.; meadow fescue; YELLO (1995); scattered along roadsides, especially along Northeast Entrance road

Lolium perenne L.; perennial ryegrass, English ryegrass; YELLO (1925); Mammoth and a few scattered locations

Phleum pratense L.; timothy, common timothy; MONT (1897), YELLO; widespread on northern range and spreading from many additional locations

Poa annua L.; annual bluegrass; MONT (1922), YELLO; disturbed areas, thermal areas, and along many backcountry trails

Poa bulbosa L.; bulbous bluegrass; YELLO (1972); Mammoth and Bechler Ranger Station

Poa compressa L.; Canada bluegrass; YELLO (1938); widespread

Poa palustris L.; fowl bluegrass; MONT (1922), YELLO; widespread

Poa pratensis L.; Kentucky bluegrass; MONT (1897), YELLO; widespread

Polypogon monspeliensis (L.) Desf.; rabbitfoot grass; MONT (1922); Mammoth area in wetlands

Puccinellia distans (L.) Parl.; weeping alkaligrass, European alkaligrass; YELLO (1926); occasional

Secale cereale L.; cultivated rye; YELLO (1989); planted in adjacent national forests after 1988 fires leading to some casual seeding in park, not persisting

Setaria viridis (L.) Beauv.; green bristlegrass; YELLO (1952); rarely appearing along roadside near Gardiner, not persisting

Triticum aestivum L.; cultivated wheat; YELLO (1991); rare along roadsides and not persisting

HYPERICACEAE

Hypericum perforatum L.; common St. Johnswort, Klamath weed; YELLO (1973); listed noxious by MT; a few infestations, especially in Lower Geyser Basin

LABIATAE

Dracocephalum thymiflorum L.; thyme-leaved dragonhead; YELLO (1990); established at several sites along roadsides

Galeopsis ladanum L.; hemp nettle; YELLO (1954); a few scattered sites

Glecoma hederacea L.; ground-ivy, gill-over-the-ground; YELLO (1974); persisting in Mammoth lawns

Lamium amplexicaule L.; common dead-nettle, henbit; YELLO (1952); a few areas near Gardiner and Stephens Creek

Nepeta cataria L.; catnip, catmint; YELLO (1952); perhaps planted historically in the Mammoth area, persisting along building edges

Salvia nemorosa L.; sage, violet sage; YELLO (1978); 1 plant eradicated near the North Entrance

LEGUMINOSAE

Medicago lupulina L.; black medic, hop clover; YELLO (1952); widespread along roadsides, thermal areas, and other locations

Medicago sativa L. var. *falcata* (L.) Doell; yellow alfalfa; YELLO (1994); plant eradicated along roadside

Medicago sativa L. var. *sativa*; alfalfa; YELLO (1952); occasional roadside plants, spreading only at lowest elevations

Melilotus albus Medikus; white sweet-clover; YELLO (1952); roadsides, especially on northern range

Melilotus officinalis (L.) Pallas; yellow sweet-clover; YELLO (1952); widespread on northern range and at other scattered locations around park

Onobrychis viciifolia Scop.; saintfoin, sandfain; YELLO (1990); isolated plants along roadside

Trifolium aureum Pollich; yellow clover, large hop clover; YELLO (1992); a few small sites scattered along roadsides

Trifolium campestre Schreber in Sturm; hop clover; YELLO (1995); Midway Geyser Basin and Potts Hot Springs

Trifolium hybridum L.; alsike clover; RM (1899), YELLO; widespread and spreading

Trifolium pratense L.; red clover, rose clover; RM (1899), YELLO; scattered locations

Trifolium repens L.; white clover, Dutch clover; RM (1899), YELLO; widespread and spreading

Vicia cracca L.; bird vetch; YELLO (1996); at least 2 roadside plants eradicated

MALVACEAE

Alcea rosea L.; hollyhock; YELLO (1993); perhaps planted historically, appeared and eradicated in parking area in Mammoth

Malva neglecta Wallr.; common mallow; YELLO (1992); 1 plant eradicated at Old Faithful

Malva rotundifolia L.; roundleaved mallow; YELLO (1989); 1 plant eradicated at Stephens Creek

OLEACEAE

Fraxinus pennsylvanica Marsh.; green ash; YELLO (1995); planted in Gardiner and escaping, 1 tree eradicated

OXALIDACEAE

Oxalis dillenii Jacq.; Dillen's wood-sorrel, gray-green wood-sorrel; YELLO (1991); a few scattered locations

Oxalis violacea L.; violet wood sorrel; US (1881); only known report, Denton (1973) states probably introduced

PLANTAGINACEAE

Plantago lanceolata L.; buckhorn plantain, ribwort; YELLO (1953); occasional in disturbed areas

Plantago major L.; broadleaf plantain, nippleseed; YELLO (1926); occasional in disturbed areas

POLYGONACEAE

Polygonum aviculare L.; prostrate knotweed, doorweed; US? (1885), YELLO; widespread, first collected by Frank Tweedy (Tweedy 1886, Rydberg 1900)

Polygonum convolvulus L.; wild buckwheat, dullseed, cornbind; RM (1899), YELLO; disturbed areas at Stephens Creek, Old Faithful, and rarely along roadsides

Polygonum lapathifolium L.; willow weed, pale smartweed; YELLO (1991); a few scattered small sites

Rumex acetosella L.; sheep sorrel, red sorrel; RM (1904), YELLO; widespread and naturalized

Rumex crispus L.; curly dock, sour dock; YELLO (1924); occasional near roads and developed areas

Rumex patientia L.; patience dock; YELLO (1924); Madison Junction

PORTULACACEAE

Portulaca oleracea L.; common purslane, mother-of-millions; YELLO (1991); spreading in Upper, Lower, and Midway geyser basins and other thermal areas

RANUNCULACEAE

Ranunculus acris L.; tall buttercup; YELLO (1998); listed noxious by MT; small infestations at Bechler Ranger Station and on northern range

Ranunculus repens L. var. *repens*; creeping buttercup; YELLO (1991); established in lawn at Mammoth

Ranunculus testiculatus Crantz; bur buttercup, hornseed buttercup; YELLO (1988); spreading around Mammoth Hot Springs and the North Entrance

ROSACEAE

Potentilla argentea L.; silvery cinquefoil; YELLO (1972); Madison Junction

Potentilla norvegica L.; rough cinquefoil, Norwegian cinquefoil; YELLO (1925); widespread in disturbed areas

Potentilla recta L.; sulphur cinquefoil; YELLO (1992); listed noxious by MT; a few scattered infestations

Prunus avium L.; sweet cherry; YELLO (1992); 1 plant on roadside thermal ground, eradicated

Pyrus malus L.; cultivated apple; YELLO (1992); a few shrubs along roadside

RUBIACEAE

Galium mollugo L.; wild madder, great hedge bedstraw; YELLO (1996); 2 sites along roadside in Lamar Valley

Galium verum L.; yellow bedstraw, lady's bedstraw; YELLO (1978); 1 site in Mammoth

SALICACEAE

Salix fragilis L.; crack willow; YELLO (1995); planted in Gardiner and escaping, 1 shrub eradicated in Yellowstone

SCROPHULARIACEAE

Linaria dalmatica (L.) Miller; Dalmatian toadflax; YELLO (1957); listed noxious by ID, MT, WY; major infestation in the Mammoth and Gardiner area (unconfirmed report that it may have been planted historically at Mammoth) and small infestations in several other areas

Linaria vulgaris Miller; yellow toadflax, butter and eggs; YELLO (1933); listed noxious by ID, WY; scattered infestations especially in the southern portion of the park

Verbascum thapsus L.; common mullein, wooly mullein, flannel mullein; YELLO (1953); well established on Mammoth Terraces and at other scattered locations

Veronica arvensis L.; corn speedwell, common speedwell; YELLO (1974); well established throughout the Upper, Lower, and Midway geyser basins

Veronica biloba L.; bilobed speedwell; YELLO (1994); Bechler Ranger Station, Mammoth, and Heart Lake

SOLANACEAE

Hyoscyamus niger L.; henbane, hog's bean; YELLO (1942); listed noxious by ID; Mammoth

Lycium barbarum L.; matrimony vine, teavine; YELLO (1987); probably originally planted around Mammoth and occasionally spreading

Solanum physalifolium Rusby var. *nitidibaccatum* (Bitter) Edmonds; hairy nightshade; YELLO (1952); Stephens Creek

UMBELLIFERAE

Carum carvi L.; caraway; RM (1905), YELLO; occasional along Northeast Entrance road

Conium maculatum L.; poison-hemlock; YELLO (1989); listed noxious by ID; established in Mammoth along Officer's Row

Daucus carota L.; wild carrot, Queen Anne's lace; YELLO (1999); one roadside plant eradicated near Midway Geyser Basin

Pastinaca sativa L.; common parsnip; YELLO (1952); Stephens Creek, not recently relocated

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MANAGING A COMPLEX EXOTIC VEGETATION PROGRAM IN YELLOWSTONE NATIONAL PARK

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ABSTRACT.—The number of documented exotic plants in Yellowstone National Park has increased from 85 known in 1986 to over 185 today. Exotic plants are substantially impacting the park's natural and cultural resources and are a high management priority. We have adopted an integrated weed management approach with regard to exotic vegetation, emphasizing prevention, education, early detection and eradication, control, and, to a lesser degree, monitoring. The program involves over 140 staff with program expenditures averaging approximately $190,000 annually. Prevention actions include requiring approved gravel on construction projects; banning hay in the backcountry and allowing transport of only certified weed-seed-free hay through Yellowstone; requiring construction equipment to be pressure-cleaned prior to entering the park; and native species revegetation after road, housing, and other construction projects have disturbed ground.

Over 4500 acres, primarily along roadsides and in developed areas, are surveyed annually in early detection efforts with emphasis placed on eradicating small, new infestations of highly invasive species such as sulfur cinquefoil (*Potentilla recta* L.) and leafy spurge (*Euphorbia esula* L.). Control efforts focus on about 30 priority species, such as spotted knapweed (*Centaurea maculosa* Lam.), oxeye daisy (*Chrysanthemum leucanthemum* L.), and hoary cress (*Cardaria draba* [L.] Desv.) using chemical, mechanical, and cultural techniques. A total of 2027 acres were treated during 1998, whereas control efforts for 12 species occurred on 2596 acres during the previous 3-year period, 1995–1997. Strong and expanding partnerships with other federal, state, and local agencies and private companies contribute to management efforts within the park. Future program goals emphasize increases in base funding to ensure continued weed management efforts as well as expanding survey, monitoring, and reclamation efforts. Ultimately, a more rigorous assessment of program effectiveness is desired.

Key words: exotic vegetation, Yellowstone National Park, integrated weed management.

The number of documented exotic plants in Yellowstone National Park (YNP) has increased from 85 recognized in 1986 to over 185 today, which represents about 15% of the vascular plant species in the park (Whipple 2001). Thirty of these plants are listed as noxious in 1 of 3 states (Wyoming, Montana, and Idaho) in which YNP is located. Some extremely invasive exotics that have not been found in Yellowstone, including yellow starthistle (*Centaurea solstitialis* L.) and purple loosestrife (*Lythrum salicaria* L.), are becoming serious problems in some adjoining states. On the other hand, nonnative plants that are not listed as noxious, like timothy (*Phleum pratense* L.), may be affecting native biotic communities to a greater degree than those plants deemed "noxious" (Wallace and Macko 1993).

Many biologists consider exotic plant establishment to be the largest threat to the integrity of native plant communities of the park. Nonnative plants have been demonstrated to negatively impact ecosystem structure and function by altering soil properties and related processes (Lacey et al. 1989, Olson 1999), plant community dynamics and related disturbance regimes (e.g., D'Antonio and Vitousek 1992), and distribution, foraging activity, and abundance of native ungulates (Trammel and Butler 1995, Thompson 1996) and small mammals (Kurz 1995). Geothermal habitats unique to Yellowstone have been altered by exotic plants, potentially compromising the long-term persistence of populations of Ross bentgrass (*Agrostis rossiae* Vasey), a restricted endemic plant found only in a few geothermal environments within the park. Aesthetics and viewsheds of cultural landscapes and historic districts within the park have been altered by the establishment of exotic plant species.

In response to the threat exotic plants pose to YNP's native flora and fauna, and in compliance

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with legal and policy mandates prescribing weed control, YNP has established an aggressive program to prevent, eradicate, and control the spread of exotic plants. This program is guided by the Yellowstone National Park Exotic Vegetation Management Plan (NPS 1986). The park's Resource Management Plan (NPS 1998) lists exotic plants as one of the major threats to natural resources.

Here we describe the structure and implementation of the exotic vegetation management program in the park, summarize distribution and area information as a result of monitoring efforts for a select group of species under control, and identify actions to enhance long-term program effectiveness. For consistency here and with Whipple (2001), all plant species nomenclature follows Dorn (1992) and is provided upon initial reference to a particular plant species. Where current usage may differ from Dorn (1992), synonomy is also provided in accordance with nomenclature used by the Weed Science Society of America.

SITE

YNP is the 1st national park in the world and represents the core of the largest, nearly intact, natural ecosystem in the temperate zone of the earth. The park has been recognized as a United Nations Biosphere Reserve and a World Heritage Site. Established in 1872, the park was set aside as a "public park, or pleasuring ground" for "the preservation, from injury or spoliation, of all timber, mineral deposits, natural curiosities, or wonders within . . . and their retention in their natural condition" (1871 Bill S. 392). Through subsequent legislation and administrative guidelines, including the National Park Service Management Policies (NPS 1988), YNP's fundamental goal continues to be the preservation of its natural and cultural resources while allowing human visitation and enjoyment.

Encompassing 2,221,722 acres (3472 square miles), YNP is located primarily in the northwestern corner of Wyoming, with portions extending into southwestern Montana and southeastern Idaho. Ninety-nine percent of the park remains undeveloped (NPS 1991). While the overall footprint of developments is small, developments, including 370 miles of paved roads, 17 frontcountry developed areas, 2200 frontcountry campsites, 300 backcountry campsites, and 950 miles of backcountry trails, are widely dispersed throughout the park. Visitation approaches 3 million people annually; about 28,000 people spend one or more nights in backcountry campsites. YNP also hosts approximately 8000 backcountry stock use nights annually.

The park consists of 5 more or less distinct vegetation zones influenced most heavily by the interaction between geology and climate (Despain 1990). Four of the 5 zones are at higher elevations between 6500 and 11,000 feet, are underlain by bedrock of volcanic andesite or rhyolite origin, and receive greater amounts of precipitation ranging from 20 to 70 inches annually. These areas generally support forests dominated by lodgepole pine (*Pinus contorta* Dougl. ex Loud.), Engelmann spruce (*Picea engelmanii* Parry ex Engelm.), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), or whitebark pine (*Pinus albicaulis* Engelm.) interspersed with subalpine meadows or alpine tundra above timberline. The remaining zone, primarily along the Yellowstone and Lamar River valleys in the northern portion of the park, encompasses some 198,000 acres (9%) of the total park area. This low-elevation zone (5200 to 6500 feet) is underlain by glacial debris of volcanic andesite and sedimentary composition and receives less precipitation (11 to 20 inches annually). As a result, the area is dominated by sagebrush (*Artemisia* spp.) steppe and grasslands and is bordered by Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) forests. This cold-desert environment provides habitat conditions most susceptible to exotic plant invasion and establishment relative to other vegetation zones in the park. These lower elevations support large wintering herds of elk (*Cervus elaphus nelsoni* Bailey) and smaller numbers of wintering bison (*Bison bison* L.), whereas mule deer (*Odocoileus hemonius hemonius* Rafinesque), pronghorn antelope (*Antilocapra americana americana* Ord), and bighorn sheep (*Ovis canadensis canadensis* Shaw) are observed mostly during the summer or at the lowest elevations during winter. Moose (*Alces alces shirasi* Nelson) can occasionally be observed throughout the year.

PROGRAM ORGANIZATION AND RESPONSIBILITIES

The National Park Service (NPS) is mandated to prevent exotic plant introduction and to control established exotic plants by law, executive order, and management policy (e.g., Executive Order 13112, National Park Service Management Policies [NPS 1988], Federal Noxious Weed Act of 1974 [NPS 1996]). YNP's size and ecological complexity require an effective organizational structure to develop and implement the exotic plant management program. The Exotic Plant Management Committee, composed of District Resource Operations Coordinators (ROC), the Branch Chief–Resource Operations, the Vegetation Management Specialist, and the Park Botanist, coordinates the parkwide program. The committee establishes parkwide prevention, early detection, eradication, and control priorities and protocols; establishes, tests, and refines inventory and monitoring techniques; acquires the necessary approvals for herbicide use and reports annual levels of herbicide use; seeks program funding and participates in partnership development and implementation; develops staff training workshops; and represents the park weed management program at various local, state, and federal workshops.

The Weed Management District is the core of program implementation. The park is divided into 4 weed management districts (Fig. 1) based on ecological and administrative criteria. Each district is supervised by a district ROC. The North District has an assistant ROC due to the number, size, and complexity of exotic plant invasions in the low elevations of the district. ROCs are responsible for local program development: setting district priorities within the framework of parkwide priorities, managing the district budget, hiring and training staff, coordinating district prevention and education programs, surveying and controlling exotic plants, and recording weed management activities.

District ROCs also participate in the establishment and implementation of weed management areas (WMA) with cooperating agencies across park boundaries within their respective districts. YNP is currently a partner in 4 multijurisdictional WMAs established in accordance with the Greater Yellowstone Coordinating Committee's Guidelines for Coordinated Management of Noxious Weeds in the Greater Yellowstone Area (GYCC Guidelines; Free et al. 1990). The Henrys Fork, Upper Madison, Upper Gallatin, and Jackson Hole WMAs were established as ecologically definable areas, irrespective of management jurisdiction, where similar weed problems exist within WMA boundaries (Fig. 2). Such recognition allows more specific weed management goals and a sharing of resources among differing administrative entities with similar weed problems.

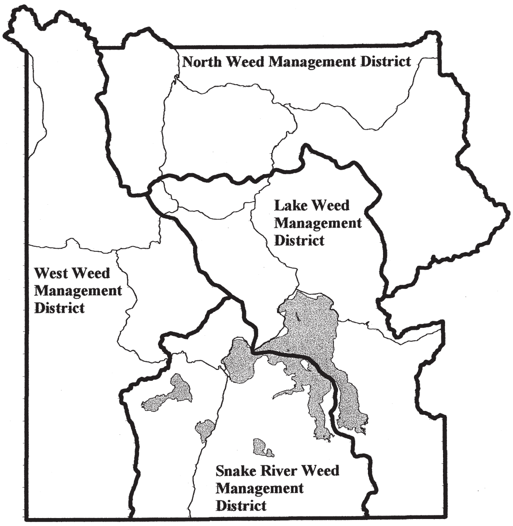

Fig. 1. Weed management district boundaries (bold lines), Yellowstone National Park.

Cooperation and participation from a variety of different individuals and park divisions are necessary for a successful weed management program in the park. Over 140 NPS staff participate in the program each year. Field and entrance station rangers assist with mechanical control of weed infestations and weed prevention by conducting hay and construction equipment inspections at entrance gates. Maintenance Division staff assist with weed prevention by cleaning construction equipment and using approved gravel in park sanding operations and construction projects. The Branch of Landscape Architecture oversees park revegetation efforts and assists with funding the exotic plant program by administering Federal Lands Highway Program funds. The Concessions Office, in conjunction with major park concessionaires, facilitates weed control in areas affected by concessionaire operations. Interpretation rangers assist with exotic plant education efforts. More than 100 short- and long-term volunteers assist annually with early detection surveys, mechanical control, and seed collection for revegetation.

Many partners from outside YNP also contribute to the program. Scientists from universities in Wyoming, Montana, and Idaho and the U.S. Geological Survey Biological Resources

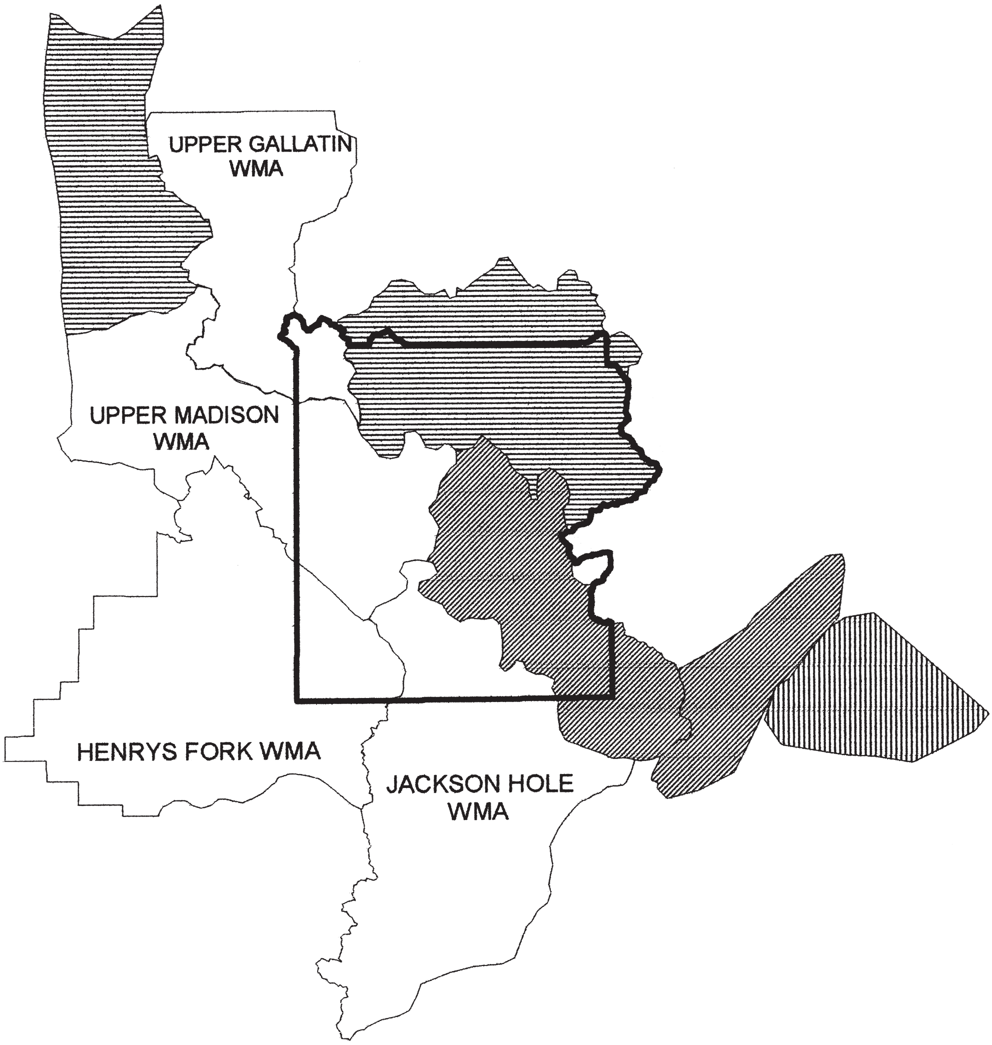

Fig. 2. Established and proposed (shaded areas) coordinated weed management areas of the greater Yellowstone region in relation to Yellowstone National Park (bold line).

Division are conducting research into the biology of weed infestations and control methods, recommending best prevention and control techniques, and assisting with staff education programs (e.g., Whitson et al. 1992). Dow AgroSciences and Monsanto have donated funding and herbicides for research, and have assisted with assessing and monitoring weed problems in portions of the park. Weed supervisors from counties that adjoin YNP are consulted regularly regarding local weed management issues.

Securing appropriate funds to support the weed management program has been challenging. Permanent employees with weed oversight responsibility are funded through NPS base operating funds. All other aspects of the program, including seasonal biological technicians, equipment, supplies, and operating funds, must be funded through opportunistic, nonrecurring funding sources with no guarantee of future funding. Total annual expenditures for the weed program are approximately $190,000. Since 1994 the Federal Lands Highway Program has funded weed monitoring and control efforts along road segments under construction. From 1994 to 1999 annual funding averaged $80,701 and ranged from $16,629 to $98,624. Funds for employee housing construction also pay for some weed control. An employee housing plan and environmental assessment (NPS 1992) states, "Two percent of actual building costs will be set aside for control and prevention of exotic plant infestations" due to the potential for invasive plants to become established after ground disturbance. Between 1995 and 1999 annual funding averaged $16,544 and ranged from $0 to $26,160. Amfac Parks and Resort, the largest park concessionaire, contracts with NPS weed managers to control weeds on concessions land assignments within park boundaries. From 1996 to 1999 annual funding averaged $2,356 and ranged from $2,275 to $2,700. In 1998 and 1999 the park safety committee provided $2,200 and $2,700, respectively, to purchase safety equipment necessary for the exotic plant management program. In fiscal year 2000 the park committed $65,000 of Recreational Fee Demonstration Program funds to control weeds.

PROGRAM IMPLEMENTATION

YNP adopted an integrated strategy to manage exotic plants. Integrated weed management encompasses preventing weed introduction, early detection and eradication of new weed infestations, controlling and/or containing established weed infestations, educating park employees and the public about weed identification and management, and inventory and monitoring to define the extent of weed problems and assess program effectiveness (Mullin 1992, Sheley et al. 1999a).

Preventing Weed Introduction

Prevention is recognized as an initial and effective weed management strategy and requires identification of problem areas and sources of seed introduction. The vast majority of YNP's noxious weed infestations occur along park roads and in developed areas where ground-disturbing activities frequently take place. Weed seeds are transported on vehicles, equipment used in construction, and in sand and gravel used for construction and maintenance. While we have not addressed private vehicles as weed seed vectors, we are establishing a prevention program aimed at reducing weed seeds in gravel and on construction equipment. All gravel used in YNP must now either come from a source operating under an approved weed management plan or be heated to 300°F prior to being used in the park. Park weed managers are working with local county weed supervisors and gravel pit owners to inventory gravel pits for weeds, develop weed management plans, and inspect the pits after plan implementation to monitor weed status. In addition, all equipment used in ground-disturbing construction must be pressure-washed and inspected prior to entering the park.

Recreational stock, as well as native ungulates, can also introduce and spread weeds. Seeds can be transported on animal hides or may pass through digestive systems. Weed seeds can also be dispersed through horse feed and hay. Opportunistic surveys associated with stock site inventories have not revealed high levels of noxious weeds in backcountry horse sites, and so we do not require that horses be quarantined prior to entering the park as some authors recommend (Sheley et al. 1999b). We do, however, ban all hay from being taken into the backcountry and allow only certified weed-seed-free hay to be transported through the park. YNP's Superintendent's Compendium specifies that

> only weed-free pellets, cubes and/or grain, but no hay, may be taken into and used in the backcountry. Certified weed-free hay, securely wrapped, may be transported through the park for use outside the park when a permit has been obtained from the Superintendent (36 CFR 1.7[B], Section 2.16 [g]).

Even certified weed-free hay is not truly "weed-free." It is only free of weeds listed as "noxious" in its home state. The hay can legally contain many nonnative plants, including timothy, clover (*Trifolium* spp.), and yellow sweetclover (*Melilotus officinalis* [L.] Pallas), that can become established and compromise native plant communities.

A vigorous native plant community is one of the most effective means of preventing invasion and spread of nonnative plants. We target native species revegetation on about 200 acres each year, primarily in association with road, housing, and other construction projects. Revegetation efforts have focused on careful preservation of topsoil as a growing medium and native seed source. Topsoil management is augmented by the park seed bank established in partnership with the Natural Resources Conservation Service Plant Materials Center in Bridger, Montana. Since 1987, seed has been collected within the park and increased at the center. Seeding is done with this seed on a site-specific basis (NPS 1997).

Early Detection and Eradication of New Weed Infestations

When prevention fails, the best course of action is to identify and eradicate new species or infestations before they become well established and disperse seeds for the 1st time. We use early detection survey routes along park roads and in developed areas to accomplish this. Each year as weeds are beginning to emerge (generally June and early July), surveys are undertaken on about 4500 acres for weed infestations in the early stages of establishment. Early detection and eradication efforts are directed at 32 of 185+ nonnative plants in Yellowstone, those species that are assigned to the watch list, priority I, or priority II category (Table 1).

Controlling and/or Containing Established Weed Infestations

Many noxious weeds and nonnative plants have become firmly established in YNP because prior attempts at prevention and early detection efforts were ineffective, eradication efforts have failed, or, in the case of some nonnatives, past management practices have led to planting and protecting these species. Since the seeds of plants can remain viable for decades (e.g., oxeye daisy seeds have germinated after 39 years; Sheley and Petroff 1999), areas where weeds have dispersed seeds must be revisited for control for years, even if no plants are apparent. Thus, we have established an ongoing weed control and/or containment program that focuses on problem areas (primarily along roadsides and developed areas) and some 30 high-priority species (priority I, II, and, in limited cases, priority III species [Table 1]). Most of these high-priority species are listed as noxious in Wyoming, Montana, and/or Idaho. The majority of control effort is directed toward listed noxious species and aggressive and new invaders.

Most of our weed control effort is put into mechanical control—pulling, grubbing, mowing, or cutting weeds. Mechanical control is our first option in small infestations when the plant biology lends itself to mechanical control, and it is our only option in sensitive areas close to surface water and in thermal basins. In 1998 mechanical means were employed on 1551 (77%) of 2027 total acres treated for control.

Chemical control is a small, but important, part of our program. We employ 8 different herbicides reviewed and approved at the highest level of the NPS. Herbicides are used to eradicate and contain aggressive, high-priority species that do not respond well to mechanical control, or when staffing for mechanical control is limiting. Conservative chemical control techniques involve the use of the most selective herbicide for the target species and spot spraying individual plants over broadcast spraying. From 1989 to 1993 herbicide use averaged 34.5 pounds of active ingredient (lbs. a.i.) applied annually (Fig. 3). From 1994 to 1998 this annual average increased over fourfold to 158 lbs. a.i. Herbicides accounted for about 23% of the total area treated during 1998, where 476 acres were treated with 115 lbs. a.i., an average of less than 4 oz per acre.

Educating Park Employees and Visitors

Formal weed education efforts began in 1982 with development and circulation of a pocket-sized notebook of sketched illustrations of select noxious weeds. By 1986 color photographs were compiled, reproduced, and condensed into the "Ten Most Wanted" poster in an effort to help staff identify some of the park's most invasive weeds. Species targeted included spotted knapweed, oxeye daisy, common tansy (*Tanacetum vulgare* L.), common mullein (*Verbascum thapsus* L.), field bindweed (*Convolvulus arvensis* L.), and houndstongue (*Cynoglossum officinale* L.). Education efforts targeting both the visiting public and park employees have grown since that time. An article entitled "Non-native Plants Impact Ecosystem" is published each spring, summer, and fall in *Yellowstone Today,* the official park newspaper, which has a circulation of approximately 775,000. Visitors traveling through the park with horses receive *Exotic Plants: Don't Let Them Ride With You!,* a small pamphlet explaining how recreational stock users can prevent weed seeds from spreading into the park. Overnight backcountry campers receive *Beyond Road's End,* a pamphlet with 2 full pages dedicated to identifying weeds and procedures for reporting weeds found in the backcountry.

Table 1. Exotic plant priority list, Yellowstone National Park. Nomenclature follows Dorn (1992) and is consistent with Whipple (2001).

Priority category	Description	Species
Watch list	Species that have not been found in Yellowstone National Park but are known to exist nearby or species that have been found in the park but removed prior to seed dispersal.	*Centaurea* × *pratensis* Thuill. (meadow knapweed) *Centaurea solstitialis* L. (yellow starthistle) *Chondrilla juncea* L. (rush skeletonweed) *Crupina vulgaris* Cass. (common crupina) *Isatis tinctoria* L. (dyer's woad) *Lythrum salicaria* L. (purple loosestrife) *Senecio jacobaea* L. (tansy ragwort)
Priority I	Species that have produced seed in the park, but populations are small and limited in number. These species have a high probability for eradication and are cost effective to control.	*Carduus acanthoides* L. (plumeless thistle) *Centaurea diffusa* Lam. (diffuse knapweed) *Centaurea repens* L. [*Acroptilon repens* (L.) DC] (Russian knapweed) *Chorispora tenella* (Pallas) DC. (blue mustard) *Dianthus* spp. (sweet william, grass pink) *Euphorbia esula* L. (leafy spurge) *Potentilla recta* L. (sulfur cinquefoil) *Onopordum acanthium* L. (Scotch thistle) *Veronica biloba* L. (bilobed speedwell)
Priority II	Aggressive invaders, some of which are well established in some localities, but most are confined to relatively small areas at specific locations. Containment will be the primary goal for these species.	*Berteroa incana* (L.) DC. (berteroa) *Cardaria* spp. (whitetop, hoary cress) *Carduus nutans* L. (musk thistle) *Centaurea maculosa* Lam. (spotted knapweed) *Chrysanthemum leucanthemum* L. (oxeye daisy) *Cirsuim vulgare* (Savi) Tenore (bull thistle) *Convolvulus arvensis* L. (field bindweed) *Cynoglossum officinale* L. (houndstongue) *Hieracium* spp. (orange hawkweed, yellow hawkweed) *Hypericum perforatum* L. (common St. Johnswort) *Linaria dalmatica* (L.) Miller [*L. genistifolia* spp. *dalmatica* Maire & Petitm.] (dalmatian toadflax) *Melilotus officinalis* (L.) Pallas (yellow sweet-clover) *Silene vulgaris* (Moench) Garcke (bladder campion) *Tanacetum vulgare* L. (common tansy) *Verbascum thapsus* L. (common mullein, wooly mullein)
Priority III	Aggressive invaders that are dispersed over large areas of Yellowstone. Control efforts are likely to be ineffective, costly, and have deleterious effects on the park ecosystem. However, work may be done to confine the spread of these plants in sensitive areas.	*Bromus inermis* Leyss. (smooth brome) *Bromus tectorum* L. (downy brome, cheatgrass) *Cirsium arvense* (L.) Scop. (Canada thistle) *Elymus repens* (L.) Gould [*Elytrigia repens* (L.) Nevski, *Agropyron r.* (L.) Beauv.] (quackgrass) *Linaria vulgaris* (L.) Miller (yellow toadflax) *Phleum pratense* L. (timothy) *Poa* spp. (bluegrass)
Priority IV	Exotics for which no control efforts are currently foreseen. These plants, other than being nonnative, do not appear to displace native vegetation to the extent of higher-priority species. Approximately 144 species fall into this category (Whipple 2001).	

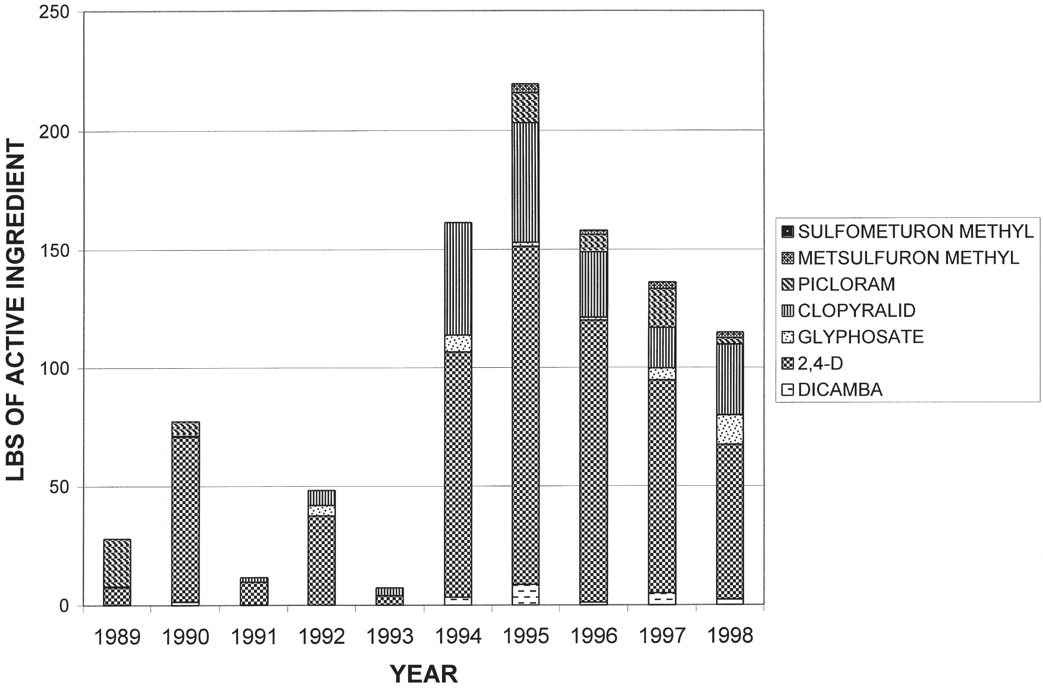

Fig. 3. Amount of herbicide, in pounds of active ingredient, applied annually from 1989 to 1998 for weed control in Yellowstone National Park.

Park employees receive updates on exotic plant identification and management at the annual Resource Management Workshop, a 3-day training session designed to share information on resource issues with park staff. In addition, the park botanist has developed a 2-hour training session on exotic plant identification that is given at field locations every 2–3 years. Since 1994, seasonal biological technicians have been required to attend a 3-day training workshop focused on weed identification and ecology, safe herbicide mixing and handling techniques, sprayer calibration, and data collection protocol. Permanent employees with weed management responsibility attend the NPS Integrated Pest Management course, maintain pesticide applicator's certification in either Wyoming or Montana, and attend continuing education courses such as state weed meetings or exotics conferences.

Inventory and Monitoring

Weed managers have emphasized the need for inventory and monitoring to quantify weed problems and evaluate program effectiveness (NPS 1986, NPS 1996, Johnson 1999). Following GYCC Guidelines (Free et al. 1990), YNP managers developed a computerized database to monitor weed management efforts. Beginning in 1993, several aspects of management actions and weed conditions were recorded in a standardized spreadsheet on an annual basis. Most information derived from the database has been for administrative purposes, i.e., quantifying the amount of time, money, and effort put forth by resource management personnel in weed management. We have made few attempts, however, to use the database to quantify weed problems or describe characteristics of weed populations throughout the park.

The YNP weed management database encompasses 31 different fields that capture yearly survey and control efforts by weed management district. Database items include the species encountered, a UTM coordinate location obtained from 7.5-minute topographic maps or global positioning satellite technology, patch size (in ft^2), a qualitative estimate of plant density (low to high), type of treatment or chemical mix/quantity where appropriate, and other secondary data relative to location (state, county, road segment, drainage, YNP jurisdictional unit, etc.). The information derives from systematic survey efforts in the developed areas and along road corridors, as well as opportunistic backcountry observations. District weed managers and technicians regularly record pertinent information on field forms during the summer season and transfer the information into a relational database (Microsoft Access) at a later date. District-wide weed information is then pooled to represent parkwide weed management activities and conditions observed within a given year. Because of this, the database captures only those weed management activities that take place within a given year and does not necessarily reflect the totality of weed conditions within the park at any one point in time. For this analysis we used parkwide independent records by site location for the years 1995–1997 to consider all known weed patches. We further focused our analysis on 15 different weed species, all of high management priority.

The database query of independent records for 15 select weed species from 1995 to 1997 revealed 1571 records covering 2596 total acres (Table 2). The North District accounted for 46% ($n = 722$) of total records and 83% ($n = 2142$ acres) of total area affected. Musk thistle (*Carduus nutans* L.), Russian knapweed (*Centaurea repens* L. [*Acroptilon repens* (L.) DC.]), spotted knapweed, oxeye daisy, field bindweed, and hoary cress occurred in greatest proportion within the North District, occupying 77–100% of the area reported for each species. On the other hand, the West District supported the greatest proportional area for common St. Johnswort (*Hypericum perforatum* L.), common tansy, and hawkweeds (*Hieracium* spp.), ranging from 51% to 99%. The West District also recorded the 2nd greatest proportional area for both oxeye daisy (22%) and spotted knapweed (14%). The Lake and Snake River districts each experienced <35 total acres across all species. Hawkweed, spotted knapweed, and musk thistle occupied 81% ($n = 27$ acres) of the total area reported for the Lake District. Weed problems in the Snake River District for the species reported here occurred primarily as scattered, isolated individuals.

Spotted knapweed was the most commonly reported species in all districts, accounting for 56% ($n = 878$) of total records and 64% ($n = 1664$ acres) of total area reported here (Fig. 4). Eighty-six percent ($n = 1424$ acres) of the area and 45% ($n = 398$) of the records for spotted knapweed were reported from the North District. Of 1664 acres parkwide, 70% ($n = 1167$ acres) were of low-density (<1 plant · 100 ft^{-2}) compared to only 8% ($n = 90$ acres) of the total area experiencing high-density (1 plant · ft^{-2}) infestations.

A frequency vs. size class distribution showed the majority (81%, $n = 714$) of records for spotted knapweed were <1 acre in size and only 3 records were for areas >100 acres. Two of these 3 records were of scattered individuals and small patches continuous with the roadside prism along major road sections. Fifty-four percent ($n = 386$) of the patches <1 acre in size were of the "incidental" variety,

Table 2. Acreage and number of records (in parentheses), by weed management district, for 12 priority weed species under control in Yellowstone National Park. Data were derived from independent records by location ($n = 1571$) for the years 1995–1997 maintained in a computerized database.

		District				
Weed species	Common name	North	West	Snake	Lake	Totals
Carduus nutans	musk thistle	70 (18)	5 (7)	<1 (2)	4 (17)	79 (44)
Hieracium spp.	hawkweeds	<1 (7)	19 (9)	<1 (8)	18 (27)	37 (51)
Centaurea diffusa	diffuse knapweed	0	<1 (8)	<1 (2)	<1 (1)	<1 (11)
Centaurea repens	Russian knapweed	3 (20)	0	<1 (1)	<1 (2)	3 (23)
Centaurea maculosa	spotted knapweed	1424 (398)	234 (305)	<1 (82)	6 (93)	1664 (878)
Tanacetum vulgare	common tansy	<1 (4)	5 (23)	<1 (13)	<1 (6)	5 (46)
Chrysanthemum leucanthemum	oxeye daisy	147 (45)	41 (71)	<1 (21)	2 (48)	190 (185)
Convolvulus arvensis	field bindweed	110 (105)	<1 (6)	<1 (1)	<1 (2)	112 (127)
Cardaria draba	hoary cress; whitetop	387 (120)	0	0	0	387 (120)
Euphorbia esula	leafy spurge	<1 (1)	<1 (5)	0	<1 (1)	<1 (7)
Potentilla recta	sulfur cinquefoil	<1 (3)	<1 (1)	0	<1 (3)	<1 (7)
Hypericum perforatum	common St. Johnswort	<1 (1)	117 (62)	<1 (4)	1 (5)	118 (72)
TOTALS		2142 (722)	421 (497)	1 (134)	32 (218)	2596 (1571)

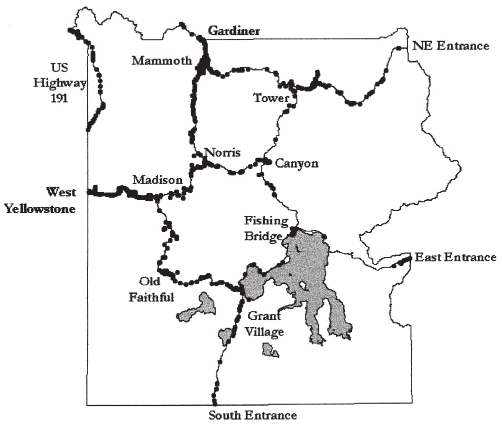

Fig. 4. Distribution of spotted knapweed in Yellowstone National Park. Data were derived from independent species records by location ($n = 878$) for the years 1995–1997 maintained in a computerized weed database.

whereby single to very widely scattered individuals were recorded in an area <400 ft^2. Although these incidental records represent a costly database item with regard to field documentation and database entry/storage, they nonetheless provide a useful index of occurrence per linear mile along major road corridors (Table 3). These data are important to assess causes and trends in spotted knapweed invasion and establishment and perhaps quantify the effectiveness of prevention and early detection components of the weed management program.

CURRENT AND FUTURE CONSIDERATIONS

The exotic vegetation management program is subject to concern, scrutiny, and controversy. While relying on mechanical, cultural, and chemical control, no active program using biological control agents is employed. Differences in management philosophy and inadequate understanding of the ecological effects of purposeful nonnative introductions (e.g., Louda et al. 1997, Strong 1997, Callaway et al. 1999) have precluded an active biological control program. Historically from 1969 to 1974, a rearing-and-release program for a defoliating moth (*Calophasia lunula* Hufn.) was attempted in the park to control dalmatian toadflax (*Linaria dalmatica* [L.] Miller [*L. genistifolia* ssp. *dalmatica* Maire & Petitm.]). The program was discontinued apparently because of poor rearing success and insufficient release stock. More recently, biocontrol agents have been released near the park, and some agents have migrated across park boundaries. Observations of ovary-feeding beetles (*Brachypterolus pulicarius* L.) have been made on both yellow toadflax (*Linaria vulgaris* Miller) and dalmatian toadflax, a capsule-feeding weevil (*Gymnaetron* spp.) was collected from yellow toadflax, and galls of seedhead-feeding flies (*Urophora* spp.) were observed on spotted knapweed. It is unlikely that biocontrol agents or emerging technologies involving plant genetics would be embraced in Yellowstone without addressing philosophical or ecological concerns weighed against current control practices.

Chemical rather than biological control generates the most controversy, ranging from appropriateness in a national park to the specific effects on wildlife, soil, and water resources. Human health and safety issues for applicators, employees, and visitors are also expressed. We try to balance these concerns with our management objectives, recognizing that (1) more passive weed management is most detrimental to overall ecosystem structure and function and has the greatest negative economic impact to individuals and agencies outside park boundaries, and (2) human health problems can be prevented. Written records are kept for areas that have been sprayed; information includes type of herbicide used and duration of human exclusion. Herbicide applicators wear full personal protective equipment, including Tyvek® suits with hoods, rubber boots and gloves, and breathing filters and goggles. We are entering into a partnership with the Environmental Protection Agency to review our herbicide storage and mixing techniques and possibly assess health effects associated with repeated herbicide handling for long-term employees in the weed control program.

Levels of herbicide use from 1994 to 1999 appear more commensurate with the degree and threat of exotic plant infestations and do not necessarily represent a continuing trend of increased reliance on herbicides for control. Rather, previous levels of herbicide use were apparently inadequate or insufficient to control incipient weed problems. Recent creative funding efforts have resulted in short-term increases in staffing, survey, and control. We anticipate a declining trend in herbicide use

TABLE 3. Number of records ($n = 386$) of spotted knapweed <400 ft^2, and an index of the number of records per mile of road, along major road segments within Yellowstone National Park.

Road corridor	Linear miles of road	Number of records	Records per mile of road
Gardiner–Mammoth	5.6	40	7.1
Mammoth–Tower	18.1	14	0.8
Tower–NE Entrance	28.7	53	1.8
Tower–Canyon	18.3	6	0.3
Canyon–Norris	11.6	15	1.3
Norris–Mammoth	20.9	68	3.3
Norris–Madison	13.3	15	1.1
Madison–West Yellowstone	13.9	9	0.6
Madison–Grant	33.5	47	1.4
Grant–S Entrance	21.5	40	1.9
Grant–Fishing Bridge	20.6	10	0.5
Fishing Bridge–E Entrance	26	5	0.2
Fishing Bridge–Canyon	15.4	9	0.6
US Highway 191	20.2	55	2.7
TOTALS	267.6	386	1.4

over time with effective control unless large areas have yet to be identified or control emphasis shifts to more ubiquitous, lower-priority species.

More active revegetation of weed-infested areas to native plant communities would similarly contribute to decreased levels of herbicide use. To date, most revegetation efforts have been directed toward reclaiming construction disturbance rather than restoring weed-infested areas. We have, however, initiated experimental trials for reclamation of lands dominated by exotic crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.), desert alyssum (*Alyssum desertorum* Stapf), and/or Russian thistle (*Salsola australis* R. Br. [*S. tragus* L.]). These areas encompass some 570 acres in the core of ungulate winter range near the gateway community of Gardiner, Montana (Houston 1982). A 125-year history of human disturbance, including hay operations for ungulate forage production, cattle grazing, channeling ground water for irrigation purposes, and railroad operations, has resulted in monocultures of exotic plant communities. Experimental trials will be used to enhance native plant reestablishment as part of an overall site rehabilitation plan.

Budget limitations require the prioritization of weed species for management purposes, preclude expanded management efforts, and cast doubt on maintaining current activity beyond the short term. Given current levels of monitoring and the structure of the weed management database, no direct measure of success can be made. The information presented here, however, will be a useful baseline from which to compare future conditions and assess program effectiveness provided comparable management effort is maintained. More emphasis on base funding would allow a structured survey and quantitative assessment of backcountry areas, inclusion of more species for aggressive control, and increased monitoring efforts to quantify the behavior of target species under control and the response of the vegetation community to herbicide application. Until then, opportunistic funding sources will be required to address these and other concerns.

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STATUS AND CONSERVATION OF SALMONIDS IN RELATION TO HYDROLOGIC INTEGRITY IN THE GREATER YELLOWSTONE ECOSYSTEM

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ABSTRACT.—Native salmonid status was evaluated with an index quantifying distribution and abundance of cutthroat trout (*Oncorhynchus clarki*) and grayling (*Thymallus arcticus*) in 41 watersheds comprising the Greater Yellowstone Ecosystem. We assessed hydrologic integrity with a percentile-based index measuring cumulative effects of reservoirs, surface water withdrawals, and consumptive water use. Status of native salmonids was poor in 70% of the watersheds; exceptions occurred in a north–south core extending from the Upper Yellowstone southward through the national parks to Bear Lake. Hydrologic integrity was highest in headwater areas and lowest in lower-elevation watersheds. Status of native and nonnative salmonid populations currently existing in the ecosystem was positively correlated with hydrologic integrity ($r = 0.58$), indicating that the hydrologic index performed well on a watershed scale in quantifying suitability of stream environments for salmonids. However, native trout status and hydrologic integrity were similarly correlated ($r = 0.63$) only when watersheds receiving the lowest possible native salmonid index score were removed from analysis because these watersheds were uniformly distributed across hydrologic integrity. We infer that nonphysical factors such as interactions with introduced fish species have played an important role in the disappearance of native salmonids. The highest priority for conservation is preservation of core watersheds, where both hydrologic integrity and native trout status are high. Restoration opportunities exist in the Teton, Idaho Falls, Willow Creek, Central Bear, and Bear Lake watersheds, where viable cutthroat trout populations remain but are threatened by habitat degradation.

Key words: Greater Yellowstone, cutthroat trout, Oncorhynchus clarki, *hydrologic alteration, watersheds, introduced species.*

The Greater Yellowstone Ecosystem (GYE) contains the headwaters of 3 continental-scale watersheds, those of the Missouri, Snake, and Green rivers. These rivers are primary tributaries, respectively, to the Mississippi, Columbia, and Colorado rivers, which, together, drain well over half of the conterminous United States. Average annual discharge from the GYE into these rivers totals 2.0 million ha-m. Rivers and lakes of the GYE are internationally famous for their recreational and scenic values; the GYE is arguably the most popular trout fishing destination in the world. Despite the economic and ecological importance of the rivers and watersheds of the GYE, there exists relatively little ecosystem-scale information on the status of these rivers and the species that inhabit them. Of 9 papers in a 1991 special section of *Conservation Biology* devoted to the GYE (Brussard 1991), none dealt with fish or other aquatic resources. Only the paper of Marston and Anderson (1991) mentioned the importance of watersheds in contributing to the ecological structure and function of the GYE. These authors concluded that spatial trends in watershed condition need to be quantified as a key step in developing ecosystem management for the GYE.

The need for an ecosystem-scale inventory of aquatic resources in the GYE has become even more critical over the past decade. The 1994 discovery of lake trout (*Salvelinus namaycush*), a nonnative species, in Yellowstone Lake illustrated that even in the center of the largest piece of relatively undisturbed land in the conterminous United States, persistence of native aquatic species is in jeopardy (Kaeding et al. 1996). In the past few years, conservation organizations have petitioned the U.S. Fish and Wildlife Service to protect under the federal Endangered Species Act all 4 subspecies of cutthroat trout (*Oncorhynchus clarki*) native to the GYE as well as the native Montana grayling (*Thymallus arcticus montanus*).

The goals of this study are to evaluate the ecological integrity of and provide conservation

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strategies at the watershed scale for aquatic systems in the GYE. In general, ecological integrity is determined by physical and biotic components. Indices of biotic integrity incorporate measures of aquatic organism assemblage structure and have been used as quick and accurate alternatives to more traditional physical- and chemical-based assessments of stream health (Karr 1981, Fausch et al. 1984, Hilsenhoff 1987). From a management perspective, however, an ideal assessment of ecological integrity should incorporate enough measures of both the biotic and physical components to allow testing of relationships between the two. If changes in the biotic component can be linked to changes in the physical component, and these, in turn, can be linked to natural resource management and use, then results of the assessment can be used to determine restoration, conservation, and management activities aimed at maintaining and improving ecological integrity.

Toward this end, we inventoried available data that could be used to assess ecological integrity of watersheds in the GYE (Van Kirk 1999, Van Kirk et al. 2000). Unfortunately, this effort failed to identify habitat and water-quality data of sufficient quantity, quality, and consistency at the watershed scale to allow development of a meaningful ecosystem-wide index of stream physical habitat condition. However, consistent U.S. Geological Survey (USGS) hydrologic data are available at the appropriate scale for all watersheds in the ecosystem, and review of the rapidly growing body of literature identifying the role of hydrologic regime in determining physical and biological characteristics of streams suggested that an index of hydrologic integrity might prove useful in quantifying the physical component of ecological integrity.

The natural hydrologic and sediment regimes of a given stream are determined by climate, geology, and topography (Gregory at al. 1991). In turn, hydrologic and sediment regimes play major roles in determining channel morphology, water temperature, and nutrient and energy fluxes. Lotic and riparian ecosystems have evolved in response to physical environment and to variability in the natural flow regime (Vannote et al. 1980, Resh et al. 1988, Poff and Ward 1989). Recent research has focused extensively on how the presence of dams and reservoirs has altered the timing and quantity of water and sediment delivered to a river system (Petts 1984, Williams and Wolman 1984, Hirsch et al. 1990), affecting both abiotic and biotic components of the riverine environment (Hill et al. 1991, Sparks 1992, Ligon et al. 1995, Collier et al. 1996). In the western U.S., reduction of peak flows, rapidly fluctuating hydropower discharges, and absence of sediment immediately below dams have been the most dramatic downstream effects of river impoundment.

As a result of altered discharge and sediment regimes, downstream channel morphology can be changed in many ways that affect stream biota. Lack of sediment in water issuing directly from a dam results in erosion of the streambed below the dam, loss of spawning gravels, streambed armoring, and stream incision (Petts 1979, Andrews 1986, Kondolf 1995). In many rivers, for example, the Colorado River below Glen Canyon Dam, warm, silt-laden water has been replaced by clear, cold water, causing a shift in the aquatic ecosystem from heterotrophic to autotrophic (Marzolf et al. 1999). Key geomorphic factors that influence river ecology and are altered by river regulation include the following: (1) cross-sectional shape, which determines the nature of habitat features such as overhanging bank cover; (2) cross-sectional size, one determinant of frequency and duration of overbank floods, which link the floodplain with the river channel and allow terrestrial/aquatic nutrient flux (Ward and Stanford 1995); (3) pool/riffle/run ratios, which determine the proportion of various habitat types available to aquatic organisms; (4) point bar and island formation, which determines availability of a variety of fish habitat; and (5) channel substrate composition, which determines, in part, invertebrate diversity and abundance and the quality and quantity of spawning gravels for fish (Petts 1984, Stanford 1994, Ligon et al. 1995).

Aquatic insect assemblage composition, diversity, and abundance are affected by quantity and timing of discharge, current velocity, substrate, temperature, and water chemistry, all of which can be modified by river regulation (Hauer and Stanford 1982, Brittain and Saltveit 1989, Casado et al. 1989, De Jalon and Sanchez 1994, Rader and Belish 1999). Hydrologic regime also determines the amount and timing of water available to streamside plants and the disturbance regime experienced by those plants. Numerous studies have documented changes in composition and abundance of riparian vegetation throughout the western states as a result of altered hydrologic regime; these changes often consist of declines in native species and establishment of exotic species (Johnson 1990, Carothers and Brown 1991, Stromberg and Patten 1991, Stromberg et al. 1993, Everitt 1995, Scott et al. 1996, 1997, Merigliano 1997, Patten 1998). Changes in riparian area structure can have substantial impacts on stream biota because of the critical functional links between terrestrial and aquatic ecosystems provided by riparian areas. For example, the riparian canopy modifies the amount of solar radiation that reaches the stream channel, affecting primary production and stream temperature. The riparian area also supplies woody debris, an important source of structural habitat in the stream channel. Several studies have examined how patterns of discharge variability and extreme high and low flow events influence fish assemblage structure (Horwitz 1978, Meffe 1984, Coon 1987, Bain et al. 1988, Jowett and Duncan 1990, Poff and Allan 1995).

Based on the importance of native salmonids in the GYE, availability of consistent watershed-scale hydrologic data across the ecosystem, and well-documented relationships between hydrologic regime and stream physical environment, we chose to utilize the status of native salmonids as the biotic index and hydrologic integrity as the physical index in our assessment. The objectives of this study are to quantify the status of native salmonid populations in the GYE, quantify hydrologic integrity of the watersheds in the GYE, assess the relationship between native salmonid status and hydrologic integrity, and develop a general strategy for conserving watersheds in the GYE.

STUDY AREA

Watersheds of the GYE

The GYE has been defined in numerous ways, but most definitions include an area of approximately 50,000 km^2 comprising Yellowstone and Grand Teton national parks and adjacent lands at elevations above 1500 m (Anderson 1991). We define the GYE as the area bounded on the east by the western edge of the Wyoming Basin ecoregion (Omernik 1987), on the south and west by the 1500-m-elevation contour and the boundary of the Middle Rockies ecoregion (Omernik 1987), and on the north by an approximate east–west line running from the Jefferson-Madison-Gallatin confluence through the Shields-Yellowstone confluence and down the Yellowstone River to its confluence with Clarks Fork (Fig. 1). Based on this definition, the GYE consists of that portion of the Middle Rockies ecoregion that lies south of the Bridger Range, the adjoining portions of the Northern Basin and Range, Snake River Basin, and Montana Valley and Foothill Prairie ecoregions (Omernik 1987) that lie above about 1500 m in elevation, and the Yellowstone River riparian corridor upstream of the Clarks Fork confluence. A substantial amount of land in the GYE is managed by public agencies other than the National Park Service, including the U.S. Bureau of Land Management and the U.S. Forest Service. Because USGS 8-digit hydrologic units (HUCs) are used as the geographic reporting unit for most water-related data, these were chosen as the basic watershed units for this study. With the exception of a few watersheds containing only a small amount of land lying within the GYE, the study area consisted of all HUCs lying wholly or partially within the GYE as defined above. This resulted in inclusion of 41 eight-digit hydrologic units (Table 1, Fig. 1). These 41 watersheds have a combined area of 162,000 km^2, which is substantially larger than most generally accepted definitions of the GYE. However, because the condition of stream biota and habitats reflects the condition of the entire watershed upstream, inclusion of lowland watersheds lying only partially within the GYE is necessary to gain an understanding of the condition of watersheds in higher elevation areas.

Salmonid Fishes of the GYE

Six species of salmonids are native to the GYE. Cutthroat trout and mountain whitefish (*Prosopium williamsoni*) are native to nearly all GYE watersheds. The Montana graying is native to watersheds of the Upper Missouri River basin. The other 3 native salmonids are endemic to Bear Lake at the southern edge of the GYE. These are the Bear Lake whitefish (*P. abyssicola*), Bonneville cisco (*P. gemmifer*), and Bonneville whitefish (*P. spilonotus*). Four

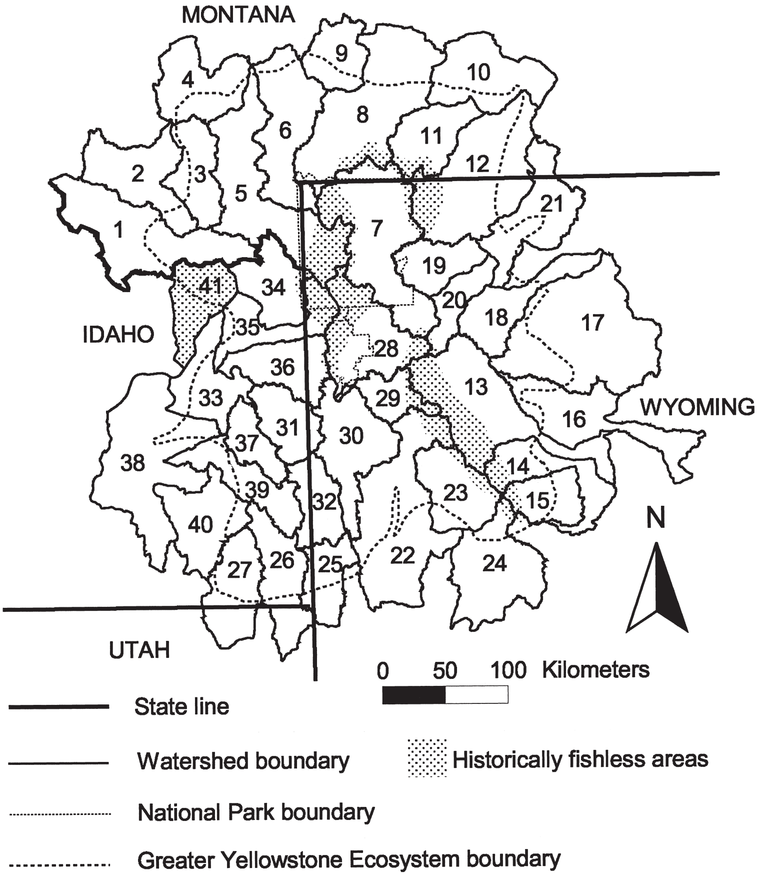

Fig. 1. Watersheds of the Greater Yellowstone Ecosystem. Shading indicates approximate location of historically fishless areas, clockwise from left: Snake River Plain sinks drainages, Yellowstone Plateau/Teton Range crest, Absaroka Range/Beartooth Plateau, and Wind River Range. Watershed identification numbers correspond to those in Table 1.

subspecies of cutthroat trout are recognized as native to the GYE. The Yellowstone cutthroat (*O. c. bouvieri*) was by far the most widely distributed of all cutthroat subspecies in the GYE, historically occupying most of the Upper Snake and Upper Yellowstone River drainages. Although the Snake River finespotted cutthroat is sometimes listed as a subspecies distinct from the Yellowstone cutthroat (Behnke 1992), this distinction has not been officially recognized taxonomically (May 1996). Westslope cutthroat (*O. c. lewisii*) are native to watersheds of the Upper Missouri basin, and Colorado River cutthroat (*O. c. pleuriticus*) are native to the Green River basin. The cutthroat subspecies inhabiting the Bear River drainage has been classified as Bonneville cutthroat trout (*O. c. utah;* Behnke 1992, Duff 1996a). However, recent genetic evidence shows that the Bear River cutthroat is more closely related to the Yellowstone subspecies than to other members of the Bonneville subspecies (Shiozawa and Evans 1995). A geomorphic explanation for this is that the Bear River became a tributary of the Great Salt Lake, the remnant of ancient Lake Bonneville, only about 30,000 years ago; prior to that time it was a tributary to the Snake River, to which the Yellowstone cutthroat is native.

The GYE contains 4 major areas that were likely barren of salmonid fish prior to Euro-American settlement: the Yellowstone Plateau/Teton Range crest, Absaroka Range/Beartooth Plateau, Wind River Range, and the entire Beaver-Camas hydrologic unit (Fig. 1). Most waters historically barren of salmonids were also barren of other fish species, with the possible exception of sculpin (*Cottus* sp.) in a few locations. Geological barriers prevented upstream migration of fish into headwater areas in the first 3 of these areas following the most recent periods of glaciation (Behnke 1992, May 1996, Varley and Schullery 1998). The Beaver-Camas watershed is part of a large region of the Snake River plain in which surface water originating in the adjacent mountains sinks into highly porous lava rock without any surface connection to the Snake River (Hackett and Bonnichsen 1994). Although it is not known with certainty whether this watershed was historically fishless, most literature (e.g., Behnke 1992, Duff 1996b) lists the watershed as historically barren of salmonids, and we will thus consider this to be the case (but see Jaeger et al. 2000).

Four species of nonnative salmonids have been introduced to the GYE. Brown (*Salmo trutta*), rainbow (*O. mykiss*), and brook (*Salvelinus fontinalis*) trout are widespread throughout the GYE. Lake trout are found in many GYE lakes and reservoirs, including Yellowstone and Jackson lakes, and golden trout (*O. m. aguabonita*) have been stocked extensively in the high mountain lakes of the Wind River and Absaroka-Beartooth ranges. Fish of all species were introduced into waters throughout the West beginning in the 1870s (U.S. Commission on Fish and Fisheries 1877), and, throughout most of the 20th century, stocking was used to provide angling opportunity in the face of increased angler numbers and decreased habitat quality. Rainbow trout have been by far the most widely utilized fish in hatchery programs, but various strains of Yellowstone cutthroat have also been stocked liberally throughout the West. Although the National Park Service ceased stocking nonnative trout in Yellowstone in 1916, it continued to stock Yellowstone cutthroat in the park until the 1950s (Varley and Schullery 1998). Hybridization with and competition from introduced salmonids have negatively affected cutthroat trout throughout the western U.S. (Krueger and May 1991). Habitat degradation associated with natural resource development and use has also been cited in the decline of native cutthroat trout (e.g., numerous papers in Gresswell 1988). Aquatic habitat in the GYE has been affected over the past 130 years by irrigated agriculture, timber harvest, livestock grazing, mining, and oil and gas exploration and extraction (Marston and Anderson 1991).

METHODS

Salmonid Status Indices

Indices of biotic integrity specific to the parameters of the GYE were developed based on concepts of naturalness proposed by Anderson (1991) and on indices utilized in the Sierra Nevada ecosystem by Moyle and Randall (1998). We assessed native salmonid status with an index based on spatial distribution and population status of native trout and grayling. We omitted the whitefish species from analysis because 3 of the species are endemic to only a single lake in the ecosystem and because consistent ecosystem-wide data on mountain whitefish populations were not available. Current and historical distribution and current population status of native trout and grayling were determined from Duff (1996b) and Varley and Schullery (1998).

For each of the 41 watersheds, we assigned a score for distribution of native trout and grayling using the following criteria:

5 = area currently occupied within the watershed deviates from area historically occupied by ≤ 20%
3 = area currently occupied within the watershed deviates from area historically occupied by 20–40%
1 = area currently occupied in the watershed deviates from area historically occupied by >40%

A score for native trout and grayling population status was assigned based on populations currently existing within their historic range in the watershed as follows:

5 = existing populations are locally abundant, natives make up majority of current trout/grayling community, all life history forms historically present in the watershed are well represented, subpopulations remain connected in metapopulations
3 = some populations may be locally abundant but nonnatives are as abundant as natives, some life history forms are not well represented, many subpopulations are isolated from others
1 = natives are rare within the watershed, existing native populations make up only a small percentage of existing trout/grayling assemblages, little or no connectivity exists among subpopulations

The native salmonid index was computed by averaging the distribution and population status

TABLE 1. Watersheds of Greater Yellowstone, the status of their salmonid fishes, and their hydrologic integrity. Salmonid status indices are interpreted qualitatively as follows: 4–5 = good, 3 = fair, 1–2 = poor. The hydrologic integrity index is interpreted qualitatively as follows: 66.7–100 = good, 33.3– 66.6 = fair, 0–33.2 = poor.

ID no.	Watershed name	USGS cataloging no.	Hydrologic subregion (major river basin)	Area (km^2)	Perennial stream (km)	Mean annual discharge (ha-m)	Native salmonid index	Existing salmonid index	Hydrologic integrity
1	Red Rock	10020001	Missouri headwaters	6,035	2,368	39,387	1	5	45.1
2	Beaverhead	10020002	Missouri headwaters	3,781	1,288	36,771	1	5	17.3
3	Ruby	10020003	Missouri headwaters	2,559	1,132	18,879	1	5	47.9
4	Jefferson	10020005	Missouri headwaters	3,504	1,445	187,557	1	4	51.1
5	Madison	10020007	Missouri headwaters	6,656	3,407	188,865	1	5	71.0
6	Gallatin	10020008	Missouri headwaters	4,714	3,239	96,296	1	5	68.3
7	Yellowstone headwaters	10070001	Upper Yellowstone	6,734	3,541	279,485	5	5	95.0
8	Upper Yellowstone	10070002	Upper Yellowstone	7,615	4,406	336,493	3	5	82.5
9	Shields	10070003	Upper Yellowstone	2,209	1,648	27,541	1	5	61.7
10	Upper Yellowstone–Lake Basin	10070004	Upper Yellowstone	4,053	1,088	631,279	1	4	82.5
11	Stillwater	10070005	Upper Yellowstone	2,745	1,422	84,660	1	5	93.8
12	Clarks Fork Yellowstone	10070006	Upper Yellowstone	7,174	2,835	93,186	1	3	50.1
13	Upper Wind	10080001	Bighorn	6,579	2,763	72,987	1	2	57.5
14	Little Wind	10080002	Bighorn	2,823	890	51,566	1	1	78.9
15	Popo Agie	10080003	Bighorn	2,067	858	28,037	1	2	70.3
16	Lower Wind	10080005	Bighorn	4,429	454	113,744	1	2	30.5
17	Upper Bighorn	10080007	Bighorn	8,936	1,557	156,709	1	2	25.4
18	Greybull	10080009	Bighorn	2,979	1,078	43,064	1	3	50.5
19	North Fork Shoshone	10080012	Bighorn	2,209	1,546	80,033	1	5	83.3
20	South Fork Shoshone	10080013	Bighorn	1,707	1,169	34,723	1	5	67.5
21	Shoshone	10080014	Bighorn	3,859	889	82,858	1	2	33.0
22	Upper Green	14040101	Upper Green	7,589	2,924	148,318	1	3	64.2
23	New Fork	14040102	Upper Green	3,160	1,168	66,250	1	4	58.3
24	Big Sandy	14040104	Upper Green	4,688	742	6,737	1	1	6.1
25	Central Bear	16010102	Bear	2,160	920	18,926	3	4	10.8
26	Bear Lake	16010201	Bear	3,160	768	71,340	3	3	10.8
27	Middle Bear	16010202	Bear	3,134	1,026	103,132	1	2	14.5
28	Snake headwaters	17040101	Upper Snake	4,351	2,098	265,665	5	5	79.8
29	Gros Ventre	17040102	Upper Snake	1,652	836	57,284	5	5	95.0
30	Greys-Hobock	17040103	Upper Snake	4,066	2,140	409,295	5	5	84.8
31	Palisades	17040104	Upper Snake	2,370	1,245	625,726	4	5	77.0
32	Salt	17040105	Upper Snake	2,297	1,190	70,408	3	4	83.3

33	Idaho Falls	17040201	Upper Snake	2,953	519	690,137	4	4	42.8
34	Upper Henrys	17040202	Upper Snake	2,823	973	136,102	2	5	76.8
35	Lower Henrys	17040203	Upper Snake	2,694	1,019	187,557	1	3	64.9
36	Teton	17040204	Upper Snake	2,927	1,230	74,813	4	4	65.0
37	Willow	17040205	Upper Snake	1,671	1,065	10,548	4	4	40.0
38	American Falls	17040206	Upper Snake	7,659	3,158	800,697	2	3	32.4
39	Blackfoot	17040207	Upper Snake	2,797	1,221	33,032	2	2	22.4
40	Portneuf	17040208	Upper Snake	3,419	1,088	24,975	1	1	24.9
41	Beaver-Camas	17040214	Upper Snake	2,543	873	3,251	1	2	33.3

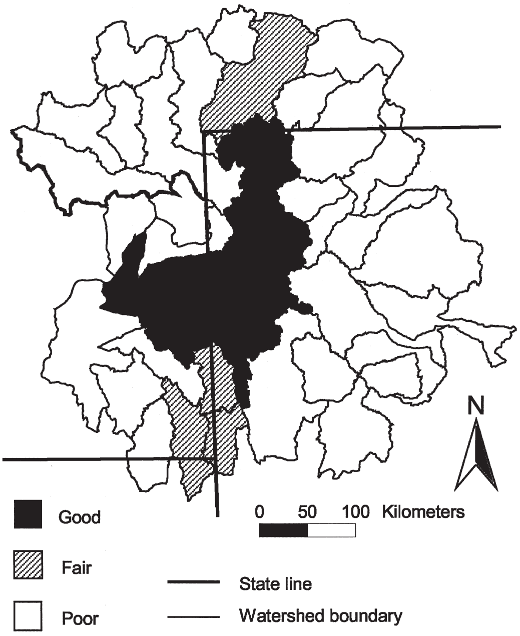

Fig. 2. Status of native trout and grayling by watershed.

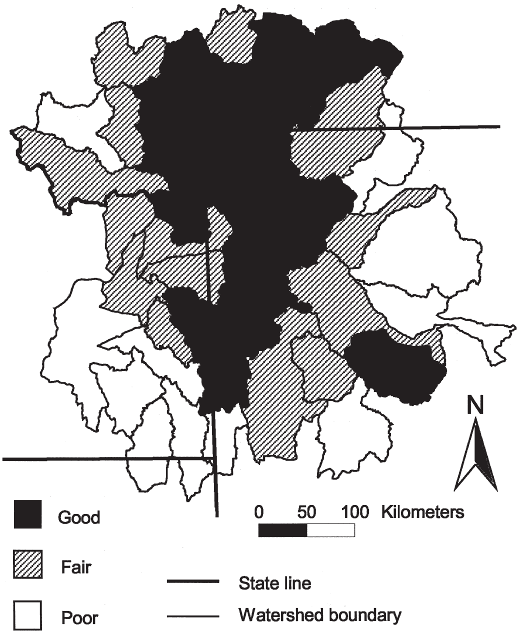

Fig. 3. Hydrologic integrity by watershed.

scores. Average scores of 4 and 5 were considered good, 3 was considered fair, and 1 and 2 were considered poor.

A 2nd index was computed to determine the status of salmonids currently existing in each watershed, whether or not the species present are native, introduced, or hybrids of native and introduced species. We refer to this index hereafter as the "existing salmonid" index. Data for determining this index came from state fish and game agencies in Idaho, Montana, Wyoming, and Utah and from federal agencies responsible for fisheries management in Yellowstone National Park and on the Wind River Indian Reservation. These data were primarily contained in unpublished agency fisheries inventory and management reports, although information gained through personal communications with fisheries biologists and managers was also used. The existing salmonid index was computed in a manner analogous to that for native species. Distribution scores were assigned exactly as for the native species, except that all presently occurring trout species were included. For example, in an area historically containing native trout and/or grayling, a score of 5 would be given if trout and grayling of any species currently occupy 80–100% of the area originally occupied by trout and grayling, even if the current occupants are nonnative species. We assigned a population status score to existing trout and grayling populations (native, nonnative, and/or hybrid) where they currently exist according to the following criteria:

5 = abundant, populations generally stable and wild
3 = moderately abundant, some populations are supplemented by stocking, population size is limited by water quality and habitat in some locations
1 = low abundance, many fisheries are supported by stocking, habitat degradation limits population abundance over large areas

The existing salmonid index was calculated by averaging these distribution and population status scores.

Hydrologic Integrity Index

An index of hydrologic integrity was computed for each watershed by determining cumulative impacts of water resource development and use in the entire drainage area upstream from the bottom of the watershed. Because all watersheds within the GYE have experienced at least some degree of hydrologic alteration and because there is no absolute scale on which to measure hydrologic integrity, the index is based on percentile rankings and thus compares each watershed to the least altered watershed in the ecosystem. We used 3 parameters reported in the U.S. Geological Survey water use database: total reservoir surface area, total surface water withdrawals, and total consumptive water use. For all but headwater HUCs, determining cumulative impacts involved totaling water use figures for the HUC in question as well as for all HUCs lying upstream, with 2 exceptions: (1) the surface area of a reservoir marking the downstream boundary of the HUC was not included in the cumulative reservoir surface area, and (2) cumulative reservoir surface area for a tributary, the confluence of which marked the downstream boundary of the HUC in question, was not included.

All cumulative totals were divided by mean annual discharge from the given HUC to obtain normalized values. Mean annual discharge was determined from USGS stream discharge data at the recording station located nearest the downstream boundary of the HUC. For normalized reservoir surface area figures, watersheds with 0 surface area were assigned a score of 0 and removed. We then assigned remaining watersheds a score based on their percentile rank. These scores were subtracted from 100 so that watersheds with 0 reservoir surface area received a score of 100, and scores decreased as relative reservoir surface area in the watershed increased. Water use figures were percentile-ranked and results subtracted from 100. Hydrologic integrity index was computed as the mean of the 3 reverse-percentile figures. Hydrologic integrity scores from 0 to 33.2 were considered poor, those from 33.3 to 66.6 were considered fair, and those of 66.7 and above were considered good. We assessed correlation between salmonid status and hydrologic integrity with Spearman's rank correlation test incorporating correction for ties.

Conservation Strategy and Priority

Conservation strategy and priority were determined based on the concepts in Moyle and Sato (1991) and Frissell (1997). These concepts state loosely that (1) existing native species should be protected where they already exist in viable populations, (2) restoration should be undertaken first in areas where it is possible to return species assemblages to historical condition without unreasonable efforts such as removing a large dam, (3) large, high-integrity watersheds can act as sources of native species to recolonize adjacent 2nd-tier watersheds as they are restored, and (4) some watersheds will never be restored to historical condition with any reasonable amount of effort and are thus better suited for appropriate management to enhance or maintain recreational, scenic, or water resource values. Such management may include stocking sport fish and maintaining popular nonnative sport fisheries. Conservation strategy and priority were assigned based on the status of native and existing salmonids and on hydrologic integrity according to the criteria in Table 2.

RESULTS

The status of native salmonids was good in 8 of 41 watersheds (20%), fair in 4 (10%), and poor in the remaining 29 (70%; Table 1). All watersheds in which native salmonid status was either good or fair occurred in the Upper Yellowstone, Upper Snake, and Bear River basins (Fig. 1). All salmonids native to these watersheds, including the endemic Bear Lake whitefishes, were present in viable populations. Yellowstone cutthroat are found throughout much of their original range in the GYE, but few viable populations exist east of the Yellowstone and Snake River headwaters areas. Viable populations of Bear River cutthroat are found in Bear Lake and a few of its tributaries and in the Smiths and Thomas Fork drainages along the Idaho-Wyoming border.

Native salmonid status was poor in all watersheds historically containing either Colorado River cutthroat or westslope cutthroat and grayling. The Montana grayling is essentially extinct in the GYE; it is found in its native range in only a few lakes in the Red Rock watershed and has been introduced in other lakes scattered throughout the GYE. A small remnant population of fluvial grayling exists in the Bighole watershed west of the GYE. Westslope cutthroat are found in a few isolated enclaves in the Red Rock, Ruby, Madison, and Gallatin drainages. Colorado cutthroat exist in numerous but generally disconnected headwater streams along the eastern slopes of the Gros Ventre and Wyoming ranges. A majority of the streams and lakes in all of the historically fishless areas now contain introduced salmonid species.

The status of all salmonid species (native, introduced, and/or hybrids) currently existing in GYE was substantially better than that of native species. Existing salmonid status was good in 24 watersheds (59%), fair in 6 (15%), and poor in only 11 (27%; Table 1). Eighteen watersheds in which native salmonid status was poor received a score of fair or good for the status of their nonnative salmonids. These watersheds are characterized by salmonid distributions that are not substantially different from those occurring historically and by viable populations of wild trout displaying varied life history patterns. However, the majority of trout populations in these watersheds comprise nonnative species rather than natives.

Because the hydrologic integrity index is a percentile-based measurement, the distribution of watersheds among the good, fair, and poor status classes was roughly uniform, as expected (Table 1). However, spatial distribution of hydrologic integrity was not uniform. All watersheds with a high degree of hydrologic integrity were located in headwater areas, and all but 2 (Little Wind and Popo Agie) occurred in a large, contiguous region in the north central part of the ecosystem centered on the national parks (Fig. 3). Those with poor scores were located at lower elevations around the perimeter of the GYE, where reservoirs, withdrawals, and consumption have resulted in substantial alteration of natural hydrologic regimes.

The population status of both native and existing salmonids was positively correlated with hydrologic integrity. With all 41 watersheds included in the analysis, native salmonid index was weakly but significantly correlated with hydrologic integrity index (Spearman's $r = 0.27$, $P = 0.041$). However, the 26 watersheds receiving a native salmonid index score of 1 (the lowest score possible) were nearly uniformly distributed across hydrologic integrity scores (Fig. 4, Table 1). With these 26 watersheds removed from analysis, the correlation between the native salmonid index and the hydrologic integrity index increased substantially

TABLE 2. Criteria for assigning conservation priority and strategy.

Native salmonid status	Existing salmonid status	Hydrologic integrity	Priority	Strategy
good/fair	good/fair	good	1 (p)	Preserve and protect
good/fair	good/fair	fair/poor	1 (r)	Rehabilitate and restore ecological processes
poor	good	good	2	Preserve and protect
poor	good	fair/poor	3	Rehabilitate and restore ecological processes
poor	fair/poor	good	4	Maintain scenic, recreational, ecological values
poor	fair/poor	fair/poor	5	Enhance scenic, recreational, ecological values

(Spearman's $r = 0.63$, $P = 0.0057$). With all 41 watersheds included, existing salmonid index was also positively correlated with hydrologic integrity (Spearman's $r = 0.58$, $P = 3.6 \times 10^{-5}$).

Based on the conservation priority and strategy criteria in Table 2, the 12 watersheds in which native trout status was either fair or good were assigned 1st priority for conservation (Table 3). The status of existing (native, nonnative, and hybrid) salmonid populations in 13 watersheds was high enough to warrant 2nd- or 3rd-tier priority for aquatic conservation in these watersheds (Table 3). The remaining 16 watersheds (39%) fell into the lowest 2 priority classifications.

DISCUSSION

The native salmonid status and hydrologic integrity indices quantify the pattern identified by Marston and Anderson (1991) of high ecological integrity in the center of the GYE and decreasing integrity with distance away from this center (Figs. 2, 3). Because the mountainous region of the GYE generally runs in a north–south orientation, the high-integrity core of the GYE consists of a central band of watersheds that extends from the Shields and upper Yellowstone watersheds on the north side of GYE southward through Yellowstone and Grand Teton national parks to the Greys and Salt rivers. Although we did not analyze our results in the context of land ownership and management, the watersheds in the high-integrity core of the GYE tend to contain large amounts of public land managed by the National Park Service and National Forest Service (Table 3). The lowest degree of ecological integrity is generally found in the nonmountainous watersheds on the west and east sides of the GYE. These watersheds generally contain large amounts of private agricultural land and rangeland managed by the Bureau of Land Management (Table 3).

The status of native salmonids across the GYE is generally poor, illustrating that even in a large, relatively undeveloped ecosystem, native fish and probably other native aquatic species are imperiled. The population status of existing native and nonnative salmonid species in the GYE is much better, indicating that in many watersheds nonnative trout species that have replaced natives are doing well. Not surprisingly, watersheds in which native species status was poor but existing species status was good support the most popular sport fisheries in the GYE for introduced brown, rainbow, brook, and cutthroat-rainbow hybrid trout. Examples include the Madison, Gallatin, Henrys Fork, Beaverhead, and North Fork Shoshone (Table 1). Habitat conditions in these watersheds are apparently good enough to support viable populations of wild trout, but the trout that currently inhabit these watersheds are nonnatives. Because our analysis was conducted on a watershed scale, it is important to note that many watersheds in which native salmonid status was poor still contain viable, but small and disconnected, populations of native trout on a local scale. Examples include Henrys Fork (Yellowstone cutthroat; Jaeger et al. 2000), Upper Green (Colorado River cutthroat; Young et al. 1996), and Greybull (Yellowstone cutthroat; Kruse et al. 2000).

Although the core of the GYE consists of large amounts of public land, much of which is protected from development in roadless and

TABLE 3. Conservation priority and primary land ownership for the watersheds of Greater Yellowstone. Land ownership is listed in approximate decreasing order of land area owned within the watershed.

ID no.	Watershed name	Conservation priority (Table 2)	Primary land ownership[a]
1	Red Rock	3	BDNF, BLM, S
2	Beaverhead	3	BLM, P, S
3	Ruby	3	P, BDNF, BLM, S
4	Jefferson	3	P, BDNF, BLM
5	Madison	2	P, BDNF
6	Gallatin	2	GNF, P, YNP
7	Yellowstone headwaters	1(p)	YNP, SNF, GNF
8	Upper Yellowstone	1(p)	GNF, P
9	Shields	3	P, GNF
10	Upper Yellowstone—Lake Basin	2	P, GNF
11	Stillwater	2	CNF, P
12	Clarks Fork Yellowstone	5	P, BLM, CNF, YNP
13	Upper Wind	5	WR, SNF
14	Little Wind	4	WR
15	Popo Agie	4	SNF, WR, BLM
16	Lower Wind	5	WR, BLM
17	Upper Bighorn	5	BLM
18	Greybull	5	BLM, P, SNF
19	North Fork Shoshone	2	SNF, YNP
20	South Fork Shoshone	2	SNF, P
21	Shoshone	5	BLM, P
22	Upper Green	5	BLM, BTNF, P
23	New Fork	3	BLM, BTNF, P
24	Big Sandy	5	BLM, BTNF
25	Central Bear	1(r)	BLM, P, TCNF, BTN
26	Bear Lake	1(r)	WCNF, TCNF, P
27	Middle Bear	5	P, WCNF, S
28	Snake headwaters	1(p)	GTNP, BTNF, P
29	Gros Ventre	1(p)	BTNF
30	Greys-Hobock	1(p)	BTNF, P
31	Palisades	1(p)	TCNF, P
32	Salt	1(p)	BTNF, TCNF, P
33	Idaho Falls	1(r)	P, BLM
34	Upper Henrys	2	TCNF
35	Lower Henrys	5	P, BLM, TCNF, YNP
36	Teton	1(r)	P, TCNF, S
37	Willow	1(r)	P, S
38	American Falls	5	P, FH, BLM
39	Blackfoot	5	P, FH, S
40	Portneuf	5	P, TCNF, BLM
41	Beaver-Camas	5	BLM, TCNF, P, S

[a] Key to land ownership: BDNF = Beaverhead-Deerlodge National Forest, BLM = U.S. Bureau of Land Management, BTNF = Bridger-Teton National Forest, CNF = Custer National Forest, FH = Fort Hall Indian Reservation, GNF = Gallatin National Forest, GTNP = Grand Teton National Park, P = private, S = state, SNF = Shoshone National Forest, TCNF = Targhee-Caribou National Forest, WCNF = Wasatch-Cache National Forest, WR = Wind River Indian Reservation, YNP = Yellowstone National Park.

wilderness areas and in the national parks, the lower-elevation areas of the ecosystem have been extensively developed, most notably for agricultural use. Because the climate in these lower-elevation areas is arid to semiarid (Marston and Anderson 1991), most agriculture is possible only with irrigation. Thus, extensive irrigation water storage and delivery systems have been developed throughout the GYE, substantially altering hydrologic regimes in the lower-elevation watersheds of the GYE. Aquatic and riparian habitat features in these more developed watersheds are likely to be degraded by other causes such as grazing, urban development, agricultural chemical runoff, sedimentation, and flood control. Thus, we expect that aquatic habitat conditions would be correlated with our index of hydrologic integrity not only because of the direct link between hydrologic regime and ecological processes but also because other types of habitat-degrading activities are likely to occur in tandem with a high

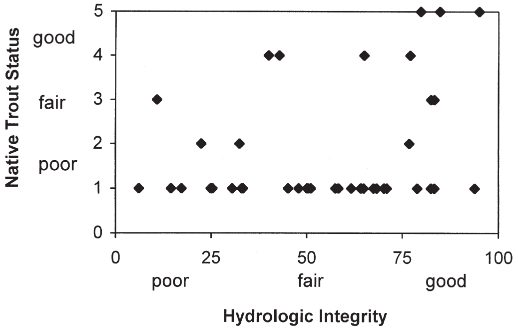

Fig. 4. Native salmonid status as a function of hydrologic integrity for 41 watersheds in Greater Yellowstone.

degree of water resource development and use.

This expectation appears to be realized in the significant positive correlation between population status of salmonid fishes and hydrologic integrity ($r = 0.58$, $P = 3.6 \times 10^{-5}$), indicating that the hydrologic integrity index performed well in quantifying the suitability of stream environments for salmonid fishes on a watershed scale. If hydrologic integrity and related environmental conditions were the only factors determining the status of native salmonids, we would expect to see an equal degree of correlation between native salmonid status and hydrologic integrity. Instead, a similar degree of correlation ($r = 0.63$) between native salmonid status and hydrologic integrity was observed only when all watersheds receiving the lowest possible native trout index score were removed from the analysis. When all 41 watersheds were included, the correlation was considerably weaker ($r = 0.27$) because the 26 watersheds receiving the lowest possible native salmonid score were nearly uniformly distributed across hydrologic integrity (Fig. 4).

Two conclusions can be deduced from these results: (1) disappearance of native salmonids from watersheds of the GYE was not due to changes in the physical environment alone, and (2) continued viability of populations of all species of salmonids (native or otherwise) is dependent on maintaining or enhancing the hydrologic integrity of watersheds in the GYE. Although habitat degradation has been an important factor leading to the decline of native cutthroat trout species throughout the West (e.g., Gresswell 1988), equally important have been the negative impacts of nonnative trout species, which include competition and hybridization (e.g., Griffith 1988, Gregory and Griffith 2000, Henderson et al. 2000). Harvest of large numbers of native fish is another factor that probably acted in concert with the spread of nonnatives to reduce native trout numbers (e.g., Gresswell and Varley 1988). However, where natives still persist, their status is positively correlated with hydrologic integrity, which, in turn, is likely to be positively correlated with aquatic habitat quality. Moyle and Randall (1998) drew similar conclusions from their study of ecologic integrity of watersheds in the Sierra Nevada. They identified introduced fish species and large dams as the 2 most important factors contributing to decline of ecological integrity. Similarly, Richter et al. (1997) reported that the 2 most important factors in the disappearance of native fish in the western U.S. are introduced species and hydrologic alteration.

Given that large-scale eradication of nonnative fish is unfeasible and that state agencies have already ceased most nonnative stocking programs in waters containing viable populations of natives, the most pragmatic approach to native trout conservation is to preserve existing populations. Thus, the 1st priority should be preventing further degradation of the GYE core watersheds that scored high in both native trout and hydrologic indices. These 7 watersheds are identified as priority 1(p) (priority = 1, strategy = preserve and protect) in Table 3, from which it is apparent that land management responsibility in these watersheds lies primarily with the National Park Service (both parks) and the Bridger-Teton, Targhee-Caribou, and Gallatin national forests. Threats from introduced trout in these watersheds (e.g., lake trout in Yellowstone Lake) should be addressed aggressively, and hydrologic integrity and habitat quality should be at least maintained, if not restored where possible. Identified in Table 3 as priority 1(r) (priority = 1, strategy = rehabilitate and restore) are the 5 watersheds that scored good or fair in the native trout index but low in hydrologic integrity. These watersheds will provide the greatest return for investment in on-the-ground restoration because they are areas where native fish are still present but suffer more greatly from habitat degradation than from nonnative species threats. These watersheds contain more private and Bureau of Land Management land than the 1(p) watersheds, although portions of the Targhee-Caribou and Wasatch-Cache national forests lie in these watersheds (Table 3). Habitat restoration in these areas is likely to involve reducing the impacts of irrigated agriculture, grazing, and flood control activities.

The watersheds in the 2nd and 3rd tiers of conservation priority are those such as the Madison, Gallatin, and Upper Henrys that provide popular nonnative angling opportunities. Preservation and restoration activities applied to both fish populations and habitat in these watersheds will provide both ecological and economic benefits. Even though these watersheds are in the 2nd- and 3rd-priority categories, they have large conservation constituencies because of the popularity of their fisheries. Generating interest in and resources for conservation work from watershed-specific recreational user groups in these drainages should be fairly easy, allowing regional and national resources to benefit the 1st-priority watersheds. Nonnative trout fisheries may be the primary beneficiaries of conservation activities in these 2nd- and 3rd-priority watersheds, but the opportunity to contribute to conservation of remnant native populations should not be overlooked. Some subbasins could be managed to maintain and/or expand the range of native trout. Land management varies widely across these watersheds (Table 3), and habitat restoration will need to address any number of issues related to agriculture, grazing, timber harvest, road construction, housing development, mining, and water management.

Watersheds in the low- and lowest-priority categories are placed there not because conservation work is not needed but because resources expended there may do little to restore native species and ecological function. However, a few like the Upper Green contain isolated remnant populations of native trout, and very specific conservation efforts have the potential to increase viability of these populations. In general, these watersheds are the most highly impacted in the GYE, and many have experienced alterations due to water resource development that may not be restored without major expenditure of resources and impacts to local communities. Conservation efforts in these watersheds should be directed toward maintaining and enhancing recreational, scenic, and water quality values, particularly those that benefit nearby cities such as Billings, Riverton, Lander, Idaho Falls, and Pocatello. Development of urban greenbelts, put-and-take fisheries in artificial ponds, and riparian protection zones are examples of cost-effective conservation measures in these watersheds. However, where possible, opportunities to restore native fish should be pursued.

An exception to this general approach to the lower-priority watersheds is restoration of what Frissell (1997) terms “grubstake habitats,” low-elevation wetland and riparian areas that are high centers of biodiversity. Large-scale restoration and preservation of these areas may be costly, but payoffs in terms of increased fish and wildlife habitat and water quality are potentially very large. Riparian areas along the lower portions of GYE’s large rivers, including the Snake, Yellowstone, Wind, Green, and Jefferson, are good examples of grubstake habitats, and large-scale watershed conservation efforts there should be implemented. Land management responsibility in the lowest-priority watersheds generally lies with private landowners, states, Native American tribes, and the Bureau of Land Management (Table 3).

CONCLUSION

The generally poor status of native salmonids in the GYE illustrates that even in an ecosystem considered to be among the most pristine and unaltered in the conterminous United States, introduced species have had detrimental impacts on native species despite the presence of high-quality habitat. Watersheds of highest ecological integrity, both in terms of native salmonid populations and hydrologic integrity, are found in the mountainous center of the ecosystem, where most of the land area and natural resources are managed by federal agencies. A practical approach to conserving watersheds and aquatic resources of the GYE is based on the observation that it is easier to maintain populations of native fish species where they currently exist than to introduce them into areas currently dominated by nonnatives. Such an approach assigns highest priority to central core watersheds, where native trout status is either good or fair. Habitat preservation and restoration in these watersheds will benefit native species without involving large-scale eradication of nonnatives. The positive correlation between the status of existing (native and nonnative) salmonid populations and hydrologic integrity in the GYE illustrates the importance of natural hydrologic function in maintaining salmonid habitat. The success of our crude hydrologic integrity index in predicting population status of salmonid fishes suggests that further development and refinement of measures of hydrologic integrity may be of great use in assessing and preserving stream biota.

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SPATIAL DISTRIBUTION OF THREE SNAIL SPECIES, INCLUDING THE INVADER *POTAMOPYRGUS ANTIPODARUM*, IN A FRESHWATER SPRING

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ABSTRACT.—The highly invasive New Zealand mudsnail, *Potamopyrgus antipodarum,* may compete with and displace native North American macroinvertebrates in freshwater systems wherever it becomes established. Densities and spatial distributions of 3 snail species including *P. antipodarum* and the threatened *Taylorconcha serpenticola* were compared among 3 adjacent habitat types (run, edge, and vegetation) in Banbury Springs, a tributary of the Snake River, near Hagerman, Idaho, USA. In all 3 habitats *P. antipodarum* was the most abundant snail species. All 3 species densities were highly variable within habitats, suggesting a nonrandom distribution pattern. Densities of *P. antipodarum* were significantly greatest in the vegetation habitat type, while densities of *T. serpenticola* were similar among habitats. Smaller-sized *P. antipodarum* were less abundant in the run habitat with its associated higher water velocities, and their densities were negatively correlated with velocity. Densities of *P. antipodarum* also were negatively correlated with distance from the highly infested, man-made Morgan Lake, while *T. serpenticola* densities were positively correlated with distance from Morgan Lake. *Potamopyrgus antipodarum* is a potential competitor with native aquatic species, although its colonization into some freshwater habitats may be limited.

Key words: threatened species, endangered species, biological invader, competition, spatial distribution.

By the mid-1980s, the exotic New Zealand mudsnail, *Potamopyrgus antipodarum* (Gastropoda: Hydrobiidae), had become established in the middle Snake River drainage and associated springs in southern Idaho, USA (Taylor 1987, Bowler 1991). It has subsequently become the dominant macroinvertebrate species in many of these waters and has spread into several river drainages in and near Yellowstone National Park, Wyoming and Montana, USA. *Potamopyrgus antipodarum* densities have been reported as high as 800,000 · m^{-2} (Dorgelo 1987). We have recorded patches of *P. antipodarum* exceeding 500,000 · m^{-2} at Banbury Springs, a tributary of the Snake River, near Hagerman, Idaho. These small patches (roughly 1 to 2 m^2) were in a spatially heterogeneous landscape and were often adjacent to patches with low densities of *P. antipodarum* (sometimes $<$1000 · m^{-2}).

It is unknown what the effects of *P. antipodarum* will be on the native macroinvertebrate communities, but given its potential for rapid population growth and its present high densities in some waters, negative ecological and associated economical impacts could occur. *Potamopyrgus antipodarum* is native to New Zealand and has become widely established throughout Europe, Australia, and now the USA. In Europe, *P. antipodarum* became established in the mid- to late 1800s and is now the dominant macroinvertebrate in many fresh to slightly saline aquatic communities (Anistratenko 1991, Cogerino et al. 1995). In the USA, *P. antipodarum* populations have been documented in (1) the Yellowstone, Madison, and Snake rivers in and near Yellowstone National Park, Wyoming and Montana; (2) the Snake River drainage, Idaho and Wyoming; (3) the Columbia River, Oregon; and (4) Lake Ontario, Canada and USA (Zaranko et al. 1997). *Potamopyrgus antipodarum* can reproduce sexually or asexually via parthenogenesis (Dybdahl and Lively 1995). Because of its ability to reproduce asexually, invading populations of *P. antipodarum* can quickly dominate an aquatic environment. Like all hydrobiid snails, *P. antipodarum* possesses an operculum, which can be used to seal itself tightly into its shell; thus, it is able to survive unfavorable conditions, including many fishes' digestive systems (Haynes et al. 1985).

The middle Snake River drainage is also home to several federally listed threatened

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and endangered snail species, including the threatened Bliss Rapids snail, *Taylorconcha serpenticola* (Rissoidea: Hydrobiidae), and the locally common pebble snail, *Fluminicola* sp. (Hydrobiidae; Bowler 1991). Very few data are available on habitat preferences and spatial distributions of any of these 3 species in the middle Snake River drainage.

For this study we collected and analyzed densities and spatial distribution data as related to 3 assumed habitat types (run, edge, and vegetation) for all 3 snail species, *P. antipodarum, T. serpenticola,* and *Fluminicola* sp., in Banbury Springs. We also related shell lengths of *P. antipodarum* with water velocity and habitat type in Banbury Springs.

STUDY SITE

Banbury Springs are located alongside the Snake River (river mile 589) at the southwestern end of the eastern Snake River Plain of Idaho, USA, and upriver of the Thousand Springs complex located at river mile 585 (Fig. 1). The Snake River runs through a steep-sided canyon within a larger trench-cut canyon through the Snake River Plain. Banbury Springs consist of 22 springs that convey water from basalt walls through an aquifer that underlies the plain. Average flow of the springs is approximately 3.5 $m^3 \cdot s^{-1}$. Surrounding acreage consists of forested wetlands, shrubland, and talus slopes. The springs form numerous braided channels that then flow into small, man-made Morgan Lake, which was created in 1965. The springs then empty into the Snake River through a culvert. Banbury Springs support several species of aquatic macrophytes, densities of which vary seasonally.

METHODS

We collected 54 small Surber samples from 3 delineated habitat types (run, edge, and vegetation) in a 30 × 30-m section of the northernmost spring at Banbury Springs between 6 April and 11 May 1999. Our small Surber sampler was a 1-mm mesh, modified Surber sampler with a collection area of 15 cm × 15 cm as compared to a 30 × 30-cm collection area used in standard Surber sampler. We elected to use the smaller Surber sampler because of the very high numbers of *P. antipodarum* collected in our samples and because a full Surber sample would often overlap from one delineated habitat type into the next. Of the 54 small Surber samples, 17 were in run habitats, 14 in edge habitats, and 23 in vegetation habitats. We delineated a run habitat as any riffle or flowing section that did not have emergent, aquatic vegetation growing and that was dominated by gravel size or larger substrates. Sample sites in runs remained free of vegetation, as of 5 November 1999. An edge habitat was that portion of the emergent aquatic vegetation habitat that was within 15 cm of a run. Vegetation habitat was defined as being more than 15 cm from a run habitat and composed of emergent, aquatic vegetation. Samples collected in the vegetation and edge habitats included both macrophytes and substrate.

To determine whether there was a relationship between size of *P. antipodarum* and habitat type, we measured 760 *P. antipodarum* shell lengths to nearest 0.05 mm: 235 from edge, 250 from vegetation, and 275 from run habitats. We measured an additional 889 *P. antipodarum* shell lengths from 12 samples in the study site from habitats with varying water velocities to determine whether there was a relationship between shell length and water velocity. Hourly water temperatures (N = 4919) were recorded at the upper and lower portions of the study site between 13 April and 5 November 1999 using HOBO temperature data loggers (Onset Computer Corp. 1998).

STATISTICAL ANALYSES

Descriptive statistics (including skewness and kurtosis), histograms, normal expected frequencies, Shapiro-Wilk W-tests, and normal probability plots of the 3 snail species densities were generated and analyzed for comparison. Densities that did not follow a normal distribution were log-normalized and reexamined. All log-normalized densities subsequently appeared to follow a normal distribution. A nonparametric Spearman rank order correlation was conducted between nontransformed *P. antipodarum* densities and water velocity. In addition, we related log-transformed *P. antipodarum* densities and water velocity using Pearson product-moment correlation. Both correlation methods were used to determine if there was a relationship between *P. antipodarum* densities and distance upstream from Morgan Lake. We also used Pearson product-moment correlation for examining the relationship

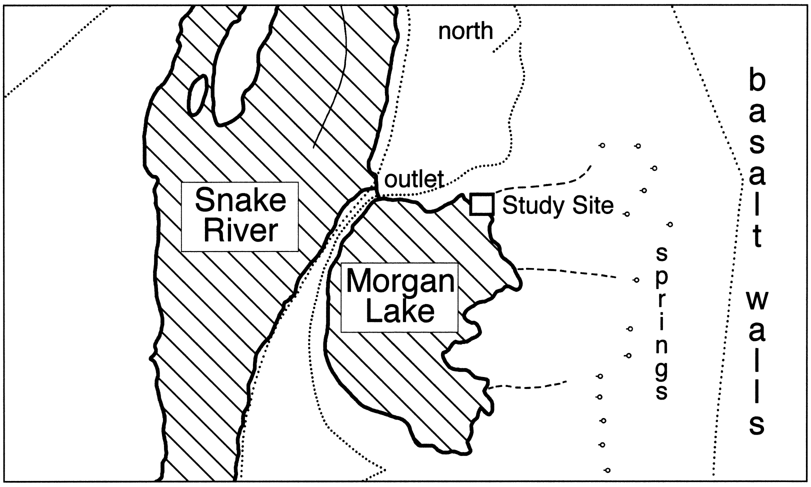

Fig. 1. Study area.

between *P. antipodarum* shell lengths and water velocity. One-way ANOVAs using Tukey HSD post hoc comparison were conducted on log-transformed densities of the 3 snail species for each species to determine if there were any differences in snail densities in the 3 habitats. *Potamopyrgus antipodarum* mean shell lengths were compared among the 3 habitats using 1-way ANOVA and Tukey post hoc comparison. We used STATISTICA for Windows (Statsoft, Inc. 1995) for all statistical analyses.

RESULTS

Potamopyrgus antipodarum had the highest densities of the 3 snail species in all 3 habitats but was more similar with *T. serpenticola* and *Fluminicola* sp. densities in the run habitat (Figs. 2, 3, 4). All 3 species densities showed a nonrandom distribution within all habitats (Shapiro-Wilk test $W < 0.01$, skewness and kurtosis > 0, and by visualization of normal probability plots) with the exception of *Fluminicola* sp. in the vegetation and run habitats (Shapiro-Wilk test $W > 0.25$, skewness and kurtosis ~0, and by visualization of normal probability plots), which showed a normal or random distribution.

Log-transformed mean densities of *P. antipodarum* were marginally different among habitats (1-way ANOVA, $F = 3.02$, df 2,26, $P = 0.07$). Mean densities (log-transformed) of *P. antipodarum* were significantly higher in the vegetation than the run habitat (Tukey HSD post hoc comparison, $P = 0.05$) but were not significantly greater in the edge than the run habitat ($P = 0.36$) or between the vegetation and edge habitats ($P = 0.53$). *Fluminicola* sp. mean densities (log transformed) were significantly different among the 3 habitats (1-way ANOVA, $F = 6.21$, df = 2,26, and $P = 0.00$). *Fluminicola* sp. mean densities were significantly greater in the vegetation and edge habitats than in the run habitat (Tukey HSD post hoc comparison, $P = 0.07$ and 0.01, respectively) but were not significantly greater between the edge and vegetation habitats ($P = 0.48$). Mean densities (log-transformed) of the threatened Bliss Rapids snail, *T. serpenticola,* were not significantly different among any of the 3 habitats (1-way ANOVA, $F = 0.63$, df = 2,26, $P = 0.53$, and Tukey HSD post hoc comparison, $P > 0.60$ for all 3 habitats), but were most variable and had the lowest median density in the vegetation habitat (Fig 4).

Water temperature was constant throughout the study site and season. Mean hourly temperatures recorded between 13 April and 5 November 1999 were 14.19°C (±0.38°C *s*; min = 12.93°C; max = 14.85°C; $N = 4919$) at the upstream portion of the study site and 14.29°C (±0.57°C *s*; min = 12.93°C; max = 16.38°C; $N = 4919$) at the downstream portion. Therefore, we did not consider temperature to be a variable in our analysis within the study site, although temperature could have an effect on snail distribution in other areas, including Morgan Lake.

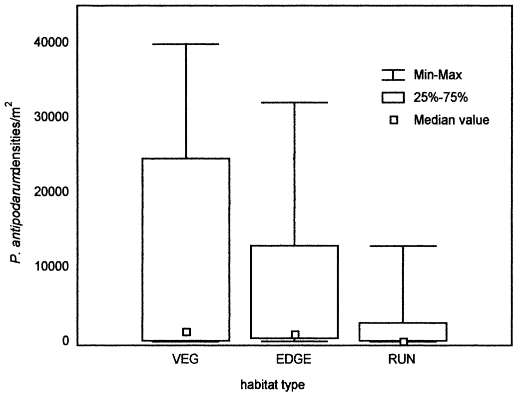

Fig. 2. Comparison of *P. antipodarum* densities · m^{-2} in 3 habitat types (vegetation, run, and edge) in the Banbury Springs study site, 1999. (Vegetation: median = 1328.04, mean = 10651.49, minimum = 0.00, maximum = 39841.20, lower quartile = 78.12, upper quartile = 24529.68, *N* = 23. Edge median = 996.03, mean = 7081.02, minimum = 39.06, maximum = 32029.20, lower quartile = 390.60, upper quartile = 12811.68, *N* = 14. Run median = 156.24 · m^{-2}, mean = 2072.48, minimum = 0.00, maximum = 12811.68, lower quartile = 78.12, upper quartile = 2460.78, *N* = 17.)

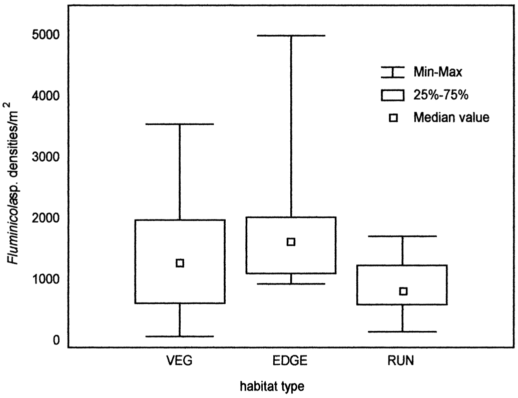

Fig. 3. Comparison of *Fluminicola* sp. densities · m^{-2} in 3 habitat types (vegetation, edge, and run) in the Banbury Springs study site, 1999. (Vegetation: median =1288.98, mean = 1448.62, minimum = 78.12, maximum = 3554.46, lower quartile = 624.96, upper quartile = 1992.06, *N* = 23. Edge: median = 1640.52, mean = 1944.63, minimum = 937.44, maximum = 4999.68, lower quartile = 1093.68, upper quartile = 2031.12, *N* = 14. Run: median = 820.26, mean = 921.36, minimum = 156.24, maximum = 1718.64, lower quartile = 585.90, upper quartile = 1249.92, *N* = 17.)

Water velocities ranged from 0 m · s^{-1} in thicker vegetation habitats to 0.52 m · s^{-1} in runs. Mean water velocity was 0.04 m · s^{-1} (±0.03 *s*) for vegetation, 0.08 m · s^{-1} (±0.12 *s*) for edge, and 0.34 m · s^{-1} (±0.15 *s*) for run habitat. Velocities were significantly different ($P < 0.05$) between run and vegetation, and run and edge habitats, but not between vegetation and edge habitats.

Non-parametric Spearman rank order correlation on nontransformed data suggested that *P. antipodarum* densities were significantly negatively related to water velocity ($N = 54$; $r = –0.52$; $P = 0.00$). Log-transformed densities of *P. antipodarum* also showed significant negative correlation with velocity using Pearson correlation ($N = 47$; $r = –0.57$; $P = 0.00$). Densities of *T. serpenticola* and *Fluminicola* sp. were not significantly correlated with velocity using nonparametric or log-transformed data analysis.

Mean shell lengths of *P. antipodarum* were significantly correlated with water velocity using Pearson correlation ($N = 12$, $r = 0.68$, $P = 0.02$). Mean shell lengths of *P. antipodarum* were also significantly greater in the run habitat than in edge or vegetation habitats ($P < 0.00$ for both), but not significantly different between edge and vegetation habitats ($P = 0.87$).

Log-transformed densities of *P. antipodarum* were negatively related with distance upstream from the pond section ($N = 60$, $r = –0.55$, $P < 0.05$), as were their nontransformed densities using nonparametric analysis ($N = 60$, $r = –0.70$, $P = 0.00$). Densities of *T. serpenticola* (log-transformed) were positively related with distance upstream from Morgan Lake ($r = 0.33$, $P = 0.03$). *Taylorconcha serpenticola* density (nontransformed) was positively related to distance from Morgan Lake ($N = 60$, $r = 0.30$, $P = 0.02$). Density of *Fluminicola* sp. was not related to distance from Morgan Lake.

Surface areas of macrophytes collected in the vegetation and edge samples were not measured in this study. Therefore, our results show only densities of snails in a 2-dimensional plane within the 3 habitats.

DISCUSSION

It appears that *P. antipodarum* may be establishing itself into the upper portion of the springs, mostly by spreading through vegetation and edges of the faster-flowing waters and

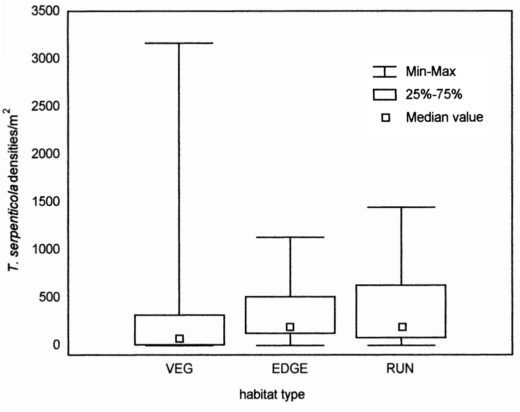

Fig. 4. Comparison of *T. serpenticola* densities · m^{-2} in 3 habitat types (vegetation, edge, and run) in the Banbury Springs study site, 1999. (Vegetation: median = 78.00, mean = 344.75, minimum = 0.00, maximum = 3163.86, lower quartile = 0.00, upper quartile = 312.48, N = 23. Edge: median =195.00, mean = 351.54, minimum = 0.00, maximum = 1132.74, lower quartile = 117.18, upper quartile = 507.78, N = 14. Run: median =195.00, mean = 353.84, minimum = 0.00, maximum = 1445.22, lower quartile = 78.12, upper quartile = 624.96, N = 17.)

then moving into new habitats, particularly unoccupied vegetation habitat. Faster water velocity possibly limits colonization of *P. antipodarum* into run habitats. The vegetation habitat with its associated slower water velocity seems to provide refuge for small-sized *P. antipodarum* and might also act as a nursery. Velocity could also affect smaller *P. antipodarum* more than larger ones due to a combination of physical, behavioral, physiological, or morphological factors. Current more easily dislodges *P. antipodarum* than *T. serpenticola* individuals. During this study, *T. serpenticola* remained attached to rock substrates when disturbed, whereas *P. antipodarum* immediately detached themselves from any substrate and readily entered the drift after disturbance. Interestingly, we found *P. antipodarum* to be the 2nd most abundant macroinvertebrate collected in 24-hour drift net samples at Banbury Springs, and we have often found them in floating vegetation mats in Morgan Lake. We have also timed their dispersal on flat substrates at up to 1 m · h^{-1}.

Continued invasions of *P. antipodarum* are likely, particularly in habitats with low water velocity and large amounts of vegetation (e.g., ponds, lakes, reservoirs, slower rivers, and backwaters), but may be limited in habitats with higher water velocities. There was little water temperature gradient in our study area, but temperature may be important for snail distribution and abundance in other aquatic environments, including Morgan Lake.

Although densities of the threatened species, *T. serpenticola,* did not vary between habitats, we do not know whether this species would be more abundant in vegetation habitats if densities of *P. antipodarum* were lower. We are presently conducting field and laboratory competition experiments between *P. antipodarum* and *T. serpenticola* and are continuing to monitor temporal and spatial changes in snail densities on a bi-monthly basis from these same locations at Banbury Springs. We will also conduct population surveys of *T. serpenticola* throughout its range in the mid-Snake River drainage in the near future.

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Article 6

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A rule-based model for mapping potential exotic plant distribution

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A RULE-BASED MODEL FOR MAPPING POTENTIAL EXOTIC PLANT DISTRIBUTION[1]

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ABSTRACT.—Wildland managers need a method to predict which portions of the lands under their stewardship are susceptible to invasion by exotic plants. We combined a database listing exotic plant species known to occur in major environmental types (habitat types) throughout the northern Rocky Mountains with a digital vegetation map of environmental types for a major national park in the region (Yellowstone National Park) to produce maps of areas potentially threatened by major exotic species. Such maps should be helpful to managers concerned with monitoring and controlling exotic plants.

Key words: maps, exotics, weeds, GIS, Yellowstone National Park, modeling, Centaurea, Cirsium, Melilotus, Phleum.

More than 100 exotic plant species occur in Yellowstone National Park (Whipple 2001), and others will undoubtedly become established in the future. Many of these are likely to undergo range expansion. An ability to predict the areas threatened by expanding exotics should be of great value to park managers trying to minimize dispersal to susceptible areas and eradicate new colonies of these areas.

Information needed to predict the potential extent of a species includes knowledge of which environments are susceptible to invasion by the species and the location and extent of susceptible environments.

Both are available for Yellowstone National Park. First, we have a map of environmental types (Despain 1990a). Students of vegetation have pointed out that plant communities provide a good indicator for site conditions (Holdridge 1947, Whittaker 1975, Huschle and Hironaka 1980). In our area Daubenmire identified major environmental types (habitat types) for eastern Washington and northern Idaho and demonstrated the relationship of indicator species to both environmental qualities (Daubenmire 1952, 1956) and plant performance (Daubenmire 1976). His environmental types have been extended into southern Idaho, Montana, and Wyoming (Pfister et al. 1977, Mueggler et al. 1980, Hironaka et al. 1983, Steele et al. 1983), and their relationships to environment have been reviewed by Weaver et al. (2001). We use environmental type as a synonym for Daubenmire's habitat type, but prefer environmental type because it unambiguously refers to physical environment and excludes confusing factors in animal "habitat" such as characteristics of a community temporarily occupying the site (e.g., species composition or structure of a seral community). Daubenmire recognized and regretted this confusion (Weaver et al. 2001).

Second, exotic species' potentials to invade environmental types representing segments of the altitudinal gradient of the northern Rocky Mountains have been identified by Weaver et al. (2001). In their treatment the environmental range of a species is expected to be wider in disturbed sites (where competition is less) than in late seral communities (where competition is intense; Daubenmire 1968, Grime 1979, Huschle and Hironaka 1980), and this has been demonstrated (Weaver et al. 2001). Thus, we expect geographic ranges of exotic species in undisturbed vegetation to be narrower than, and nested in, ranges of the same species occupying disturbed vegetation.

This paper has 5 objectives: (1) to demonstrate a method for mapping potential plant distribution, (2) to illustrate it with 4 exotic plant species of Yellowstone National Park, (3) to publicize maps of 24 other exotics, (4) to compare the mapped ranges of each species on undisturbed and disturbed sites, and (5) to

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[1] Presented at the 5th Biennial Scientific Conference on the Greater Yellowstone Ecosystem, October 1999. See footnote 1 on p. 409.

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evaluate the method by comparing predicted distributions with actual distributions recorded by Yellowstone National Park's weed management staff.

METHODS

Working in Glacier National Park, Yellowstone National Park, Grand Teton, and areas between, Weaver et al. (2001) studied the distribution of exotic plants in 16 environmental types representing altitudinal zones of the northern Rocky Mountains. To determine which exotics invade disturbed and undisturbed vegetation in these environmental types, they recorded presence at 7–10 sites in each environmental type. To test susceptibility, they examined sites long exposed to diverse seed sources, i.e., sites near major highways. Their inspection of each site was concentrated in two 4 × 25-m plots running parallel to the road. Entry into disturbed sites was examined with a plot on the roadcut (inslope) bordering the highway. Entry into near-climax vegetation was examined with another plot in adjacent undisturbed vegetation. They listed all species present in the plot (and in similar areas around it), recorded presence in five 4 × 5-m segments of the plot as an index of ubiquity, and estimated cover with 75 points located near the central axis of the plot. They reported both constancy values (the percentage of plots in an environmental type where the species occurred) and cover for each species. For a more complete description of their methods, refer to Weaver et al. (2001).

We used Weaver et al.'s (2001) constancy value as a measure of a species' ability to establish in an environmental type. Our maps indicate areas where a species was present at more than half the sites, at less than half the sites, and where they were capable of invading the climax community.

Two details require elaboration. First, because Weaver et al. (2001) did not encounter all environmental types that occur in Yellowstone National Park, we predicted exotic plant species occurrence, in those Yellowstone National Park types for which they had no data, from the most similar type for which data were available. A type was judged to be similar if it was in a similar moisture range of the same series. Resultant assignments are shown in Table 1. Exotic plant species presence in the known type was assigned to other types in its group.

TABLE 1. Environmental types of Yellowstone National Park with Weaver et al. (2001) equivalents.

Weaver et al.[a]	Yellowstone environmental type[b]
DECA/CARX	alpine tundra
FEID/AGCA	FEID/DECA
	POFR-ARCA/DECA
	ARCA/FEID
	ARTR/FEID-GEVI
	FEID/STRI
	FEID/AGCA-GEVI
	FEID/AGCA
ARTR/FEID	ARTR/FEID
ABLA/ARCO	PIAL/VASC
	PIAL/CAGE
ABLA/VASC	ABLA/LIBO-VASC
	ABLA/VAGL-VAGL
	ABLA/THOC
	ABLA/VASC-VASC
	ABLA/VASC-PIAL
	ABLA/VASC-CARU
	ABLA/CAGE
	ABLA/CARU
ABLA/ARCO	ABLA/CARO
	PICO/CAGE
	PICO/CARO
	PICO/PUTR
PSME/PHMA	PSME/PHMA
PSME/SYAL	PSME/SYAL
	PSME/CARU
	PSME/SPBE-SPBE
AGSP/BOGR	FEID/AGSP
	ARTR/AGSP
STCO/AGSP	AGSP/POSA-STCO

[a]Environmental types are named for 2 species, including a dominant overstory species and an indicator species. Names of these species are abbreviated with a 4-letter code including 2 letters from the genus name and 2 from the specific epithet: ABLA = *Abies lasiocarpa*, AGCA = *Agropyron caninum*, AGSP = *Agropyron spicatum*, ARCA = *Artemisia cana*, ARCO = *Arnica cordifolia*, ARTR = *Artemisia tridentata*, BOGR = *Bouteloua gracilis*, CAGE = *Carex geyeri*, CARO = *Carex rossii*, CARU = *Calamagrostis rubescens*, CARX = Carex spp., DECA = *Deschampsia caespitosa*, FEID = *Festuca idahoensis*, GEVI = *Geranium viscosissimum*, LIBO = *Linnaea borealis*, PHMA = *Physocarpus malvaceus*, PIAL = *Pinus albicaulis*, PICO = *Pinus contorta*, POFR = *Potentilla fruticosa*, POSA = *Poa sandbergii*, PSME = *Pseudotsuga menziesii*, PUTR = *Purshia tridentata*, SPBE = *Spirea betulifolia*, STCO = *Stipa comata*, STRI = *Stipa richardsonii*, SYAL = *Symphoricarpos albus*, THOC = *Thalictrum occidentale*, VAGL = *Vaccinium globulare*, VASC = *Vaccinium scoparium*.

[b]Weaver et al. (2001) did not encounter all environmental types that occur in Yellowstone National Park. Thus, Yellowstone types (Despain 1998) were grouped with the Weaver type to which they were most similar. Blocking in this table indicates the correspondences. Yellowstone types for which there are no equivalent Weaver types include hot springs vegetation, sedge bogs, willow/sedge, wet forests, talus, and water.

Second, Despain's (1990a) habitat type map sometimes uses mosaic mapping units that contain 2 dominant types, such as a matrix of grasslands with numerous islands of trees or vice versa. In these cases we averaged the constancy values of the 2 component types to derive a value for the mosaic units. If a species could invade the climax vegetation of either of the types, the entire map unit was considered to be susceptible to that species.

The resultant database was combined with the vegetation map using GIS to create 28 maps, one for each species studied. Four species are used as illustrations. Canadian thistle (*Cirsium arvense* [L.] Scop.) and spotted knapweed (*Centaurea maculosa* Lam.) are classed as noxious weeds by the surrounding states. Yellow sweetclover (*Melilotus officinalis* [L.] Lam.) and timothy (*Phleum pratense* L.) are crop plants that have become widely established in nonagricultural areas of the region. All 4 are of special concern to Yellowstone National Park managers.

To evaluate the success of our model, we compared locations we mapped for 3 species with actual locations mapped by Yellowstone National Park's staff: Canadian thistle, spotted knapweed, and yellow sweetclover (data for timothy were not available).

RESULTS

Potential ranges of 28 exotic species found repeatedly in northern Rocky Mountain vegetation (Weaver et al. 2001) were mapped. Maps are available from the Geographic Information and Analysis Center, Montana State University, Bozeman, website (http://www.giac.montana.edu) in raster format at 50-m resolution, which should be useful for field purposes.

Centaurea maculosa is classified as a noxious weed in the Greater Yellowstone Ecosystem. The potential range of spotted knapweed mapped for disturbed sites (Fig. 1) includes the drier portions of the park, i.e., dry grasslands/shrublands and drier Douglas-fir forests. We mapped no areas where knapweed would have an expected constancy >50%. It is expected to invade climax vegetation only in dry grasslands predominantly at low elevations. In contrast to our predictions, actual Yellowstone National Park data showed many locations along park roads outside our predicted areas. Thus, more data are required to determine how threatening this species is in Yellowstone National Park. Unpredicted locations may be either transient occurrences that would disappear without constant seeding from the outside or an indication that knapweed enters environments not predicted by this model and is thus a serious threat over a much larger area than that mapped. While it does not appear to pose a serious threat to the majority of the park, it should be closely monitored as a potential threat especially in the Yellowstone River valley along the north boundary.

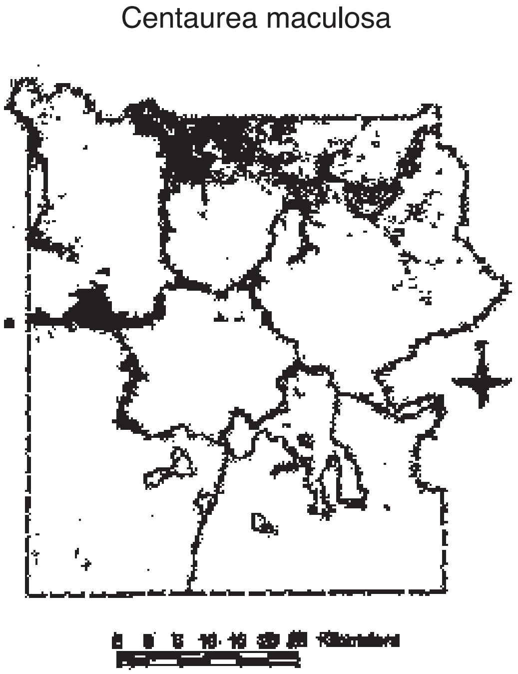

Fig. 1. Potential distribution of *Centaurea maculosa* (spotted knapweed) in Yellowstone National Park. Gray areas show the distribution of disturbed areas where it is expected to occur in less than half a series of study plots. No areas occurred where it would be capable of occurring in more than half the study plots. Black areas show distribution of those sites where it is capable of invading climax vegetation. Roads are indicated (solid line) for reference. Actual locations recorded by Yellowstone's weed management staff are shown by triangles.

Cirsium arvense is a 2nd noxious weed of the Greater Yellowstone Ecosystem. The potential range mapped for it (Fig. 2) includes disturbed areas primarily in sparsely vegetated forest types and montane and subalpine grasslands/shrublands. We map no potential for entry into dry grasslands/shrublands. Because it does not invade climax vegetation, colonies established on disturbed sites are expected to die out as succession progresses to climax. No areas occurred where Canadian thistle would have an expected constancy >50%. Our map is

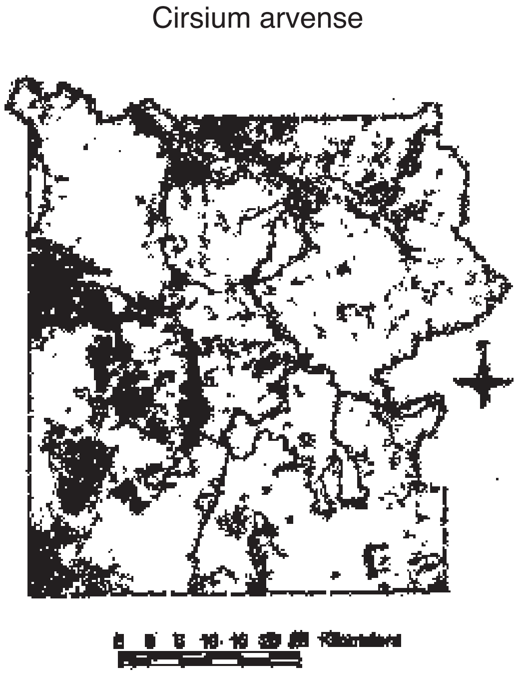

Fig. 2. Potential distribution of *Cirsium arvense* (Canadian thistle) in Yellowstone National Park. Gray areas show the distribution of disturbed areas where it is expected to occur in less than half a series of study plots. No areas occurred where it would be capable of occurring in more than half the study plots. Black areas show distribution of those sites where it is capable of invading climax vegetation. Roads are indicated (solid line) for reference. Actual locations recorded by Yellowstone's weed management staff are shown by triangles.

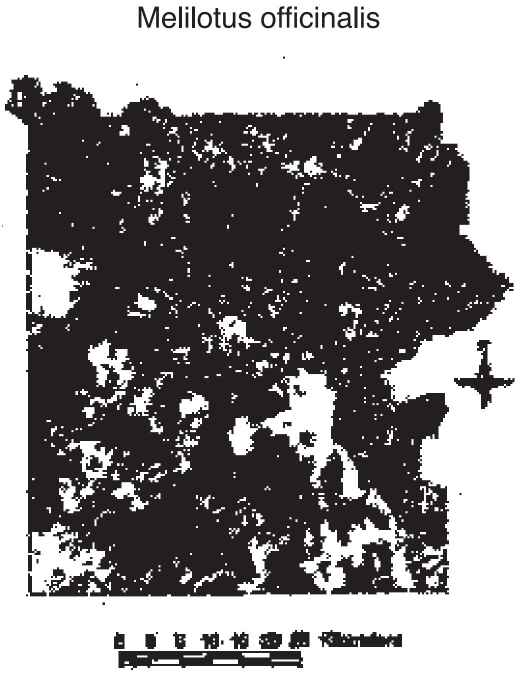

Fig. 3. Potential distribution of *Melilotus officinalis* (yellow sweetclover) in Yellowstone National Park. Gray areas show the distribution of disturbed areas where it is expected to occur in less than half a series of study plots. No areas occurred where it would be capable of occurring in more than half the study plots. Black areas show distribution of those sites where it is capable of invading climax vegetation. Roads are indicated (solid line) for reference. Actual locations recorded by Yellowstone's weed management staff are shown by triangles.

validated by noting that the majority of locations mapped by the Yellowstone National Park weed management staff are within the areas we mapped as potential habitat. Anomalous colonies in dry grassland/shrubland units may be located within inclusions of wetter environmental types.

Melilotus officinalis is a plant of special concern because it tends to dominate grasslands. The potential range mapped for yellow sweetclover on disturbed sites (Fig. 3) includes areas from drier grassland/shrubland sites in the northern part of the park to moist subalpine meadows. Our map predicts that *Melilotus* is capable of invading open climax communities across the same range. In the higher-elevation forest zone it can invade disturbed areas. No areas were mapped where yellow sweetclover would have an expected constancy >50%. Most locations recorded by the weed management staff did not correspond to predicted locations. More data must be gathered to determine the threat posed by yellow sweetclover. This species could become a serious problem if it displaces native climax species in sites to which it is well adapted.

While *Phleum pratense* is less obvious than the forbs just discussed, it has a significant tendency to dominate Yellowstone National Park vegetation (Weaver et al. 2001). The potential range mapped for timothy (Fig. 4) includes disturbed areas in most of the park. The map indicates that it can invade climax communities in a smaller range of environmental types, i.e., moister grasslands/shrublands and lower forest communities. It is more common than spotted knapweed, Canadian thistle, and yellow sweetclover on disturbed sites; i.e., it had a constancy >50% over large portions of the park. Because weed management staff

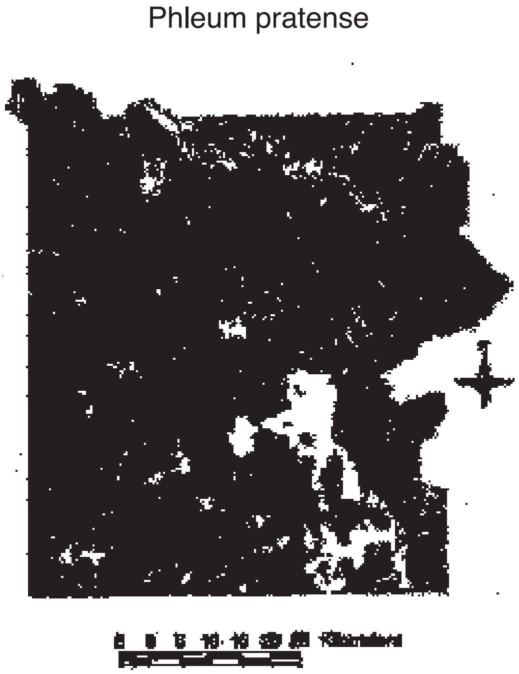

Fig. 4. Potential distribution of *Phleum pratense* (timothy) in Yellowstone National Park. Light gray areas indicate where it is expected to occur in less than half a series of study plots. Dark gray indicates areas where it is expected to occur in more than half the study plots. Black areas show distribution of those sites where it is capable of invading climax vegetation. Roads are indicated (solid line) for reference.

members do not map it, actual location data for this widespread species are not available for validation of our maps. While it is of little concern in the forested types because it would be greatly reduced at canopy closure, it could be of major concern in moister grassland/shrubland environments, which are the major source of forage for native ungulates.

DISCUSSION

This exercise has demonstrated a method for producing maps showing the potential ranges of exotic plant species in disturbed and undisturbed environments. Some general patterns are seen in the maps: (1) potential ranges of some species are limited while others are extensive; (2) most invader species are adapted to colonize disturbed sites, and thus species ranges are broader on disturbed than undisturbed segments of an environmental type; (3) where colony locations are known, constancies are usually highest in or near the potential range predicted. We attribute near-misses to interfingering of environmental types in ecotonal areas, unmapped islands of one type in a matrix of another, or inexact records of invader colony locations made by the weed team.

The certainty of our maps could be increased by adding more observations, particularly in those types where Weaver et al. (2001) have no data. The most extensive of these in Yellowstone are the wetland types and high-elevation forests.

For simplicity we have mapped ranges in successional extremes of severely disturbed roadside cuts and near-climax conditions. Roadcuts are typically void of developed soil and are usually in the early stages of primary succession. Gathering more data relating to more moderate disturbances, such as wildland fire, could usefully extend the work. For example, while Canadian thistle has been shown to increase after forest fire (Turner et al. 1997), this is not reflected (Fig. 2). The persistence of this species as the community succeeds, after fire, to climax vegetation deserves study. Thus, it would be useful to gather exotic species distribution data across successional stages within each of the environmental types (Despain 1990a) to allow a broader and more accurate evaluation of the threat posed by a particular species.

We recommend that managers gather the data necessary to use this method to further their efforts in monitoring and controlling the establishment and spread of these exotic plants, especially those that are most likely to cause extensive ecological and economic problems.

ACKNOWLEDGMENTS

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EXOTIC PLANTS IN EARLY AND LATE SERAL VEGETATION OF FIFTEEN NORTHERN ROCKY MOUNTAIN ENVIRONMENTS (HTs)[1]

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ABSTRACT.—We determined the capacity of exotic plants to invade major environmental types of the northern Rocky Mountains. We did this by observing their presence on disturbed and undisturbed sites in relatively well inoculated locations—corridors adjacent to highways—on transects across the mountains in Glacier National Park and Grand Teton National Park and on low-altitude sites between them. We draw 3 primary conclusions. First, of 29 exotics commonly found, the most dominant are intentionally introduced grasses (*Agrostis, Bromus, Dactylis,* and especially *Phleum pratense* and *Poa pratensis*) and legumes (*Melilotus, Medicago,* and *Trifolium*) rather than the forbs more often listed as noxious. Second, in the environmental types studied, disturbed sites are invasible, except in the alpine. Third, invasion of undisturbed sites declines from grasslands and open forests to alpine to moist forests. This gradient probably represents a decline in resource (light, water, nutrients) availability for herbs, except in the alpine, where a physical limitation is suggested by the poor performance of exotics on noncompetitive disturbed sites.

Key words: exotic plants, aliens, weeds, Phleum pratense, Poa pratensis, Bromus inermis, Bromus tectorum, Trifolium, Melilotus, Centaurea, Chrysanthemum leucanthemum, *habitat types, environmental types,* Bouteloua gracilis, Agropyron spicatum, Artemisia tridentata, Pseudotsuga menziesii, Abies lasiocarpa, *mountain meadows, alpine, seral stages, disturbance, climax, northern Rocky Mountains, Grand Teton National Park, Glacier National Park, Yellowstone National Park.*

National forests and parks have a mandate to manage against exotic plants both in their charters (U.S. Congress 1872) and recent executive directives (Clinton 1994, 1999).

Management of exotics requires their identification. Plants exotic to specific regions (e.g., Whitson 1992) and management units (e.g., Whipple 2001) have often been listed to facilitate recognition and identification. A listing by ecological zones within a region would refine this capacity.

In addition, a listing by environmental types within a region would provide a key to environments (or sites) the plant might invade or might already have invaded. Identification of occupiable environmental types will enable managers to concentrate control efforts in a fraction of the management area. Two environmental qualities are important. First, one considers environmental types (defined in Methods), determined by physical characteristics such as climate and substrate (Holdridge 1947, Daubenmire 1968, 1970, Whittaker 1975) and indicated locally by potential natural vegetation (Pfister et al. 1977, Mueggler and Stewart 1980, Steele et al. 1983). And, within each of these, one compares sites on the competitive spectrum from freshly disturbed (noncompetitive) to late seral (very competitive; Grime 1979, Despain 1990).

The objectives of this paper are thus to list the common exotics of the northern Rocky Mountains, to provide separate lists of the exotics present in major upland environmental types of the region, and to compare exotic presence in an early (less competitive) and late (more competitive) seral stage in each environmental type. A companion paper extends our results to separately map the potential distribution of major exotics on disturbed and undisturbed sites in Yellowstone National Park (Despain et al. 2001).

METHODS

Our term *environmental type* is synonymous with Daubenmire's (1968a, 1968b, 1970) *habitat type* (HT). (1) An environmental type (ET = HT) includes all environments (equivalent, but not identical) capable of supporting a climax

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[1] Presented at the 5th Biennial Scientific Conference on the Greater Yellowstone Ecosystem, October 1999. See footnote 1 on p. 409.

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association (series of plant communities of the same kind). (2) The concept is useful because it groups discrete sites (or environments as opposed to plant communities) likely to respond similarly to similar managment (Daubenmire 1968b, 1976, Pfister et al. 1977, Mueggler and Stewart 1980). (3) The term *environmental type* is preferred because it clarifies the concept that the types represent physical environment (e.g., moisture and temperature) rather than habitat for a particular organism, since the latter "habitat type" may either extend across several environmental types (e.g., wide-ranging plants in Table 3) or may not exist in the organism's optimal environmental type (e.g., if vegetation of the seral stage present provides too much competition [Walter 1960] or fails to provide necessary nutrients, cover, or structure). Daubenmire (personal communication) recognized the environmental type/habitat type confusion—especially among zoologists—and wished he had called his types "environmental types."

To determine which exotics might invade a specific environmental type (e.g., a montane environment occupied by *Pseudotsuga menziesii*/*Symphoricarpos albus* at climax), we needed to observe exotic colonization of well-inoculated sites in that type. Thus, we sampled several (7–11) sites jointly in that type and near a major highway that has long delivered seed to it (Table 1).

To determine which "seral" vegetation types in that environmental type could be invaded, we needed to compare invasion of highly disturbed (low competition), less disturbed (early seral), and high competition (late seral) sites (Grime 1979) occupying that physical environment. Thus, we sampled relatively gentle road cuts, logged right-of-way (not reported here), and nearby undisturbed vegetation at each of the 7–11 sites studied. The fact that our work was primarily in national parks facilitated location of undisturbed sites adjacent to highly disturbed sites. The relatively low establishment of a species on a late seral site, perhaps 20–30 m away, is attributed to competition but could also be due to failure to disperse. We attribute most of the deficiency to competition, however, both because differences in distances from the highway are short and because dispersal is a characteristic selected for in opportunistic species.

To complete the list of exotics likely to invade our region, we needed to sample other major environmental types representative of the environmental gradient from steppe upward through forest to the alpine. Thus, we sampled 15 environmental types along highways crossing the mountains in Glacier and Grand Teton national parks (1984–1985) and in intervening lowland areas (in 1986). We identified major environmental types by using late seral vegetation as indicators (Holdridge 1947, Daubenmire 1968a, 1968b, 1970, Whittaker 1975). While our exotic lists for major environmental types approach completeness, our regional list is incomplete because we omitted less widespread types such as those along streams or on unusual substrates. The environmental types (HTs) sampled are listed, in altitudinal order, in Table l, with abbreviations, general locations, and sample size (~10). Underlying changes in climate and soils along the gradient are compared in Table 2, as well as by Daubenmire (1968a, 1970), Pfister et al. (1977), Mueggler and Stewart (1980), and Steele et al. (1983).

Thus, our sample design included 15 environmental types (HTs), 2 treatments reported here (and 3 others [Weaver et al. 1993]), and approximately 10 replications (sites). Vegetational characteristics of each of the approximately 800 sites studied were recorded with measures of presence, frequency, and cover of both native and exotic species present. (1) Presence was recorded by listing all exotic and native plant species present in a 1 × 25-m plot representative of the zone and parallel to the highway traveled. We separately noted any other species present in adjacent similar vegetation. Natives in the plots, not discussed here, are listed in Weaver et al. (1993). (2) Cover of a species was measured by recording the percentage of 75 points covered by that species. The 75 points were located by lowering 3 pins into the vegetation in each meter point along the plot's center line. Cover was integrated over a type by averaging cover measurements across sites, but only at sites where the species occurred. We omitted unoccupied plots in these calculations to measure the success of species at sites where they did occur. If desired, cover values for the environmental zone as a whole can be calculated by multiplying cover values presented by the associated *constancy value*; this will correct the cover

TABLE 1. Environmental types (HTs), locations, and sizes of samples in which exotic distributions were observed. Environmental types are listed in approximate order of altitude, from low to high.

Environmental type (HT)[a]	Abbreviation[b]	Location[c]	Sample[d]
GRASSLANDS/ SHRUBLANDS			
Stipa comata/ Bouteloua gracilis	STCO/ BOGR	Broadwater MT	7
Agropyron spicatum/ Bouteloua gracilis	AGSP/ BOGR	Broadwater MT	8
Artemisia arbuscula/ Festuca idahoensis	ARAR/ FEID	Teton WY	10
Artemisia tridentata/ Festuca idahoensis	ARTR/ FEID	Meagher, Gallatin MT	10
Festuca scabrella/ Festuca idahoensis	FESC/ FEID	Glacier MT	10
DRY FORESTS			
Pseudotsuga menziesii/ Symphoricarpos albus	PSME/ SYAL	Meagher, Gallatin MT	10
Pseudotsuga menziesii/ Physocarpus malvaceus	PSME/ PHMA	Gallatin MT, Park WY	6
WARM MOIST FORESTS			
Populus tremuloides/ Calamagrostis rubescens	POTR/ CARU	Flathead MT	8
Tsuga heterophylla/ Clintonia uniflora	TSHE/ CLUN	Flathead MT	10
Abies lasiocarpa/ Clintonia uniflora	ABLA/ CLUN	Flathead MT	9
Abies lasiocarpa/ Xeophyllum tenax	ABLA/ XETE	Flathead MT	10
COOL CONIFER FORESTS			
Abies lasiocarpa/ Arnica cordifolia	ABLA/ ARCO	Teton WY	10
Abies lasiocarpa/ Vaccinium scoparius	ABLA/ VASC	Teton WY	10
HIGH GRASSLANDS AND TUNDRA			
Festuca idahoensis/ Agropyron caninum	FEID/ AGCA	Teton WY	10
Deschampsia caespitosa/ Carex spp.	DECA/ CASP	Park WY, Carbon MT	11

[a] Environmental types are those of Pfister et al. (1977) and Meuggler and Stewart (1980).
[b] Abbreviations provide a key to Table 3. They represent dominant species by reporting initial letters (2) from genus and species names.
[c] Locations are specified by county. Glacier and Flathead are in the Glacier National Park area. Broadwater and Meagher are adjacent to the Bridger/Big Belt Mountains. Gallatin, Park, and Carbon are at the north edge of Yellowstone. Teton includes Grand Teton National Park.
[d] Each environmental type was sampled at 7–11 sites. At each site 5 environments were sampled with 5 parallel quadrats. Of these, those representing roadcuts and undisturbed vegetation are discussed here.

value downward for sites at which the species did not occur (Table 3). (3) Constancy was calculated as the percentage of sites in the environmental type at which the species occurred.

We hypothesized that a strong presence of an exotic in roadside samples would result in a strong presence in adjacent undisturbed vegetation because a strong presence at the roadside indicates both good adaptation to the environment and production of many propagules for colonization of nearby sites. We tested this hypothesis, using both constancy and cover data, by comparing the presence of each exotic in disturbed vegetation on sites adjacent to occupied vs. unoccupied native vegetation. The Mann-Whitney test, a nonparametric *t* test, was used (Gibbons 1985). An alternative test, regression/correlation, was forgone because quantitative data from the undisturbed sites are currently unavailable.

In a companion paper (Despain et al. 2001), we map the potential range of an exotic in a region by using a map of the environmental types (HTs) of the region (e.g., Despain 1990b) as a base and shading ETs invasible by the species studied. We expect the range mapped on disturbed sites to enclose the range on undisturbed sites because competition is less rigorous on disturbed sites.

RESULTS

Our observations of exotic plant presence on roadcuts (outslopes) and adjacent undisturbed vegetation of 15 environmental types are summarized in Table 3. (1) Vertically, table segments list groups of exotic species found, according to their ranges on the altitudinal gradient studied: those with narrow, moderate, or broad amplitude and those with an interrupted range. (2) The elevational gradient ranges from dry steppe, through warm dry forests, warm moist forests, cool forests, to mountain meadows and alpine tundra. Fifteen segments (environmental types or habitat types) on this gradient are listed horizontally. These are named and characterized in Table 1. (3) Entries in Table 3 specify the presence of exotics, both on disturbed sites in corridors along which propagules are expected to move and on adjacent undisturbed sites. Presence on roadsides is indicated by constancy (the percent of occupied

TABLE 2. Comparison of environments in major Rocky Mountain ecosystems. Standard errors, as well as additional data, are available in Weaver (1978, 1980, 1990, 1994).

	Temperatures (C)[b]			Water availability (mm)[c]				
Parameter	Jan min	T_{gs} mean	July max	Pptn ann	Drt mo	HOH deficit	Soil WHC	GS[d] mo
Alpine tundra[a]	–16	6	12	778	0	0	38	3.6
Abies lasiocarpa	–18	12	22	820	0	0	30	4.5
Pseudotsuga menziesii	–16	12	27	580	0	1	103	3.6
Festuca idahoensis	–12	12	27	380	1	6	101	5.1
Agropyron spicatum	–13	12	28	380	1	17	117	4.9
Bouteloua gracilis	–15	14	31	350	2	25	117	4.4

[a] The ecosystems compared range from alpine down through high forests (ABLA), low forests (PSME), and grasslands (FEID, AGSP, and BOGR). Each is named for its climax dominant vegetation and abbreviated with initial letters from its generic and specific epithets.

[b] Temperatures (Weaver 1980, 1990) include average January minimum, growing season mean, and average July maximum.

[c] Water data include annual precipitation, drought months, and annual water deficit (Weaver 1980, 1990, 1994), and water-holding capacity of the rooted zone (Weaver 1978), all in mm.

[d] Growing season months are defined as those with moist soils and average air temperature above 0°C (Weaver 1994).

sites in the ET). Potential dominance on those sites is indicated by cover (the average cover on sites which are occupied); and current realized success is found by multiplying these entries. Presence in undisturbed vegetation is reported nonquantitatively from plots of the same size and shape. The material in cells having constancies >30% is in boldface because a higher constancy indicates that the plant has established more or less regularly in that environmental type.

The 29 exotic plants occuring in >10% of the sites in at least one environmental type are listed (Table 3, vertically). Ten species have a narrow amplitude; i.e., they have a high constancy in only 1 or 2 types. Ten species have a moderate amplitude, that is, range over 4–8 environmental types, as arranged in Table 3. Four species have a broad amplitude, ranging over 10–14 ETs. The ranges of 5 species of moderate to broad distribution are interrupted; that is, they occupy low and higher sites, but not the intervening environments. Two types of occurrence deserve further comment. First, plants with low constancy in a single ET are ignored because they may occupy microsites in an environmental type; that is, they do not actually occupy the environmental type discussed. Alternatively, they could either be new to the region (Forcella and Harvey 1981) or be the vanguard of a newly adapted ecotype. Second, 7 environmental types contain a species which occurs on undisturbed, but not on noncompetitive disturbed, sites. Such species could possibly require a stability not found at roadsides, e.g., lack of erosion or frost action. More likely, these species are "accidentals"; otherwise this pattern would repeat in similar types, as it does for *Taraxacum.*

On disturbed sites the number of high-constancy (>30%) exotics (Fig. 1, Table 3) was 10–11 in grasslands, 9–12 in dry forests, and 8–10 in warm moist forests and 7–11 in cool forests. Numbers were lower in shrublands (5–7), mountain meadows (5), and alpine (1). Numbers of low-constancy exotics were 3–6 in grasslands, 5–11 in dry forests, 3–6 in warm moist forests, and 2–6 in cool forests. Low-constancy richness was similar in mountain shrublands (2–5) and mountain meadows (7), and low in alpine (2).

The number of exotics entering undisturbed sites (Fig. 1, Table 3) decreased from grasslands (9–13) through aspen forests (8) and shrublands (5–7) to conifer forests (0). It increased again in mountain meadows (7) and alpine tundra (2). While the richness (average number of species per sample) on undisturbed sites is always lower than on disturbed sites, most grassland ETs are occupied by at least one species not found on disturbed sites in it.

DISCUSSION

Exotics in the Northern Rocky Mountains

We found only 29 exotic species (Table 3) in our sample of major upland environmental types of Glacier National Park, Grand Teton National Park, and little disturbed intervening areas including parts of Yellowstone National Park. Our list does not include species that have invaded since 1986, which occupy heavily grazed areas or uncommon substrates. To

TABLE 3. Presence of major exotic species in major environmental types[a] of the northern Rocky Mountains. Code digits[b] indicate constancy and cover on disturbed sites and tendency to invade undisturbed vegetation. Constancies >30% are in boldface to emphasize environments where the species is common.

	STCO BOGR	AGSP BOGR	ARAR FEID	ARTR FEID	FESC FEID	PSME SYAL	PSME PHMA	POTR CARU	TSHE CLUN	ABLA CLUN	ABLA XETE	ABLA ARCO	ABLA VACC	FEID AGCA	DECA CARX
SPECIES WITH NARROW AMPLITUDE															
Agropyron cristatum	**7CX**[b]	X	..	1A	..	..	..	..	..	..	..	..	..	..	..
Alyssum alyssoides	**8AX**	**9BX**	..	..	1AX	..	1A	..	..	..	..	..	..	..	..
Camelina microcarpa	**4AX**	**5AX**	..	..	..	..	..	..	..	..	..	..	..	..	..
Bromus japonicus	**8BX**	**6AX**	..	..	..	1A	X	..	1C	..	..	..	..	..	..
Descurania pinnata	**5AX**	**5AX**	..	..	..	..	..	..	..	..	..	..	..	2CX	..
Rumex acetosa	..	..	**9DX**	**9D**	..	1A	..	..	..	..	1A	..	..	..	0A
Dactylis glomerata	..	..	2B	**3B**	..	2BX	**5EX**	..	1A	..	1A	1B	2B	..	..
Festuca pratensis	..	..	..	..	..	1A	**5A**	..	..	..	..	..	..	..	..
Verbascum thapsus	2AX	1AX	..	..	2B	..	**5B**	1A	..	..	..	..	..	..	..
Chrysanthemum leucanthemum	..	..	..	..	..	..	..	..	**5B**	..	..	..	..	..	..
SPECIES WITH MODERATE AMPLITUDE															
Tragopogon dubius	**4AX**	**8AX**	1AX	**5BX**	**4AX**	2A	**5BX**	1A	1A	2B	..	1B	1A	..	..
Centaurea maculosa	**4BX**	**3AX**	**1D**	..	**7EX**	2A	..	**7C**	2B	..	..	..	..	..	..
Melilotus officinalis	**8BX**	**8BX**	..	..	**6BX**	**3B**	**5A**	**9CX**	2A	1B	1A	..	**3E**	1BX	..
Cirsium arvense	..	1A	..	..	**3CX**	**4A**	1A	**8CX**	..	..	..	1A	..	..	..
Poa compressa	1A	1A	..	..	**6CX**	1AX	1A	**8C**	1A	1A	**3A**	1A	..	1A	X
Trifolium procumbens	..	..	..	..	**4BX**	..	..	**7BX**	**7C**	**5D**	**3B**	..	..	..	..
Trifolium pratense	..	..	..	..	..	**5BX**	1AX	..	**7D**	1C	**8D**	..	..	..	..
Trifolium repens	..	..	..	..	..	**5DX**	1A	..	**8C**	**4B**	**8B**	1B	**4B**	1C	..
Agrostis alba	..	..	..	..	..	1A	..	**6DX**	**6C**	**4A**	**5B**	2B	**4B**	..	..
Trifolium hybridum	..	..	..	..	2A	1AX	..	2C	**9D**	**8D**	**6D**	**8E**	**8E**	**6C**	..
SPECIES WITH BROAD AMPLITUDE															
Bromus inermis	2B	**5E**	2B	..	**5D**	**5DX**	**8B**	2AX	**5E**	**8E**	**6B**	**7D**	**4D**	..	..
Poa pratensis	**4EX**	**5EX**	**9EX**	**9EX**	**8DX**	**7CX**	**6CX**	**7BX**	**4B**	**6C**	**7B**	**5C**	**4C**	**7DX**	..
Taraxacum officinale	X	2AX	X	**5BX**	**3B**	**8CX**	**8BX**	**8BX**	**9C**	**8C**	**5C**	**9E**	**8D**	**9CX**	**3BX**
Phleum pratense	..	..	1AX	..	**9DX**	**7CX**	**8DX**	**9EX**	**9D**	**9C**	**9C**	**8B**	**8C**	**7BX**	0A
SPECIES WITH INTERRUPTED RANGES															
Lactuca serriola	**5AX**	2BX	..	2A	..	1A	**5A**	..	..	..	..	..	..	..	..
Bromus tectorum	**9BX**	**7DX**	..	..	..	X	**3BX**	..	..	..	..	..	..	..	..
Polygonum aviculare	..	1AX	**9CX**	**4BX**	..	..	..	..	..	..	..	..	**4A**	X	..
Madia glomerata	..	..	**7AX**	**5CX**	..	1A	..	**3B**	..	..	..	**3A**	**5B**	2BX	..
Medicago lupulina	..	..	1A	..	..	**4C**	**6C**	..	..	..	..	**3C**	**4D**	**3A**	..

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[a]Environmental types are listed from dry to moist, as in Table 1: grasslands (1, 2, 5), shrublands (3, 4), dry forests (6, 7), aspen (8), warm moist forests (9–11), cool forests (12, 13), mountain meadows (14), and alpine (15).

[b]Codes indicate constancy in roadside sites, cover in occupied roadside sites, and invasiveness. Constancy (= the probability of occurring in a stand in the environment): 0 = 0–9, 1= 10–19, 2 = 20–29, . . . 9 = 90–100%. Cover classes are A = +, B = 0–1%, C = 1–2%, D = 2–5%, E = 5–25%, F = >25%. Invasion of undisturbed areas in an environmental type is indicated by X.

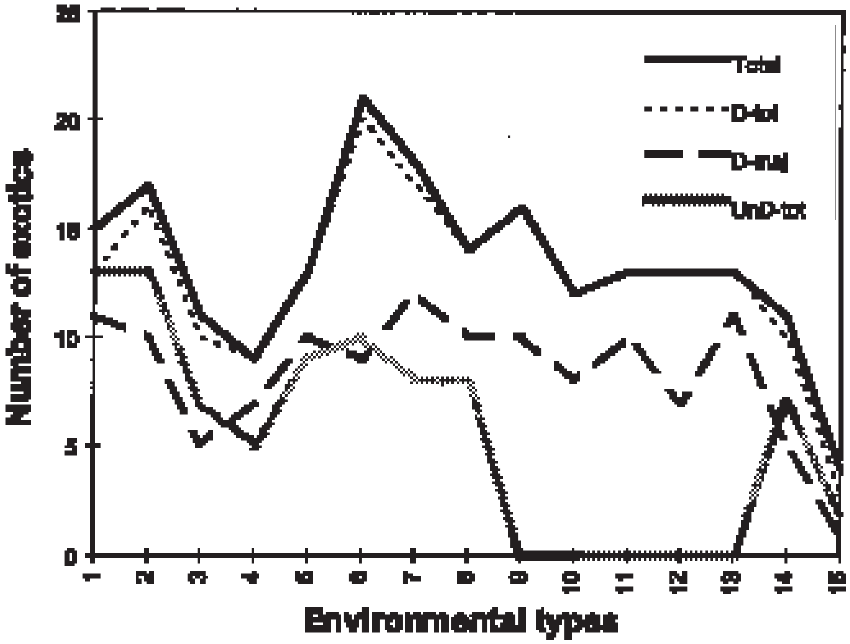

Fig. 1. Number of exotics (richness) by class and environmental type. Classes are total exotics of undisturbed sites (UnD-tot), common exotics of disturbed sites (D-maj), all exotics of disturbed sites (D-tot), and all exotics of disturbed and undisturbed sites (Total). Environmental types are as listed in Tables 1 and 3, that is, grasslands (1, 2, 5), shrublands (3, 4), dry forest (6, 7), aspen (8), warm moist forests (9, 10, 11), cool forests (12, 13), mountain meadows (14), and alpine (15).

illustrate this qualifying statement, we give *Chrysanthemum leucanthemum* as a species underrepresented because its range is expanding, *Centaurea maculosa* as less common than expected because it expands with grazing absent on the sites we studied, and *Euphorbia esula* as a species that is most important in areas moister than we sampled, e.g., riparian sites. Since volcanic materials are uncommon in the region, extrapolation to volcanic parts of Yellowstone National Park must be made with caution.

Exotic Richness Across Environmental Types

The presence of an exotic in an environmental type depends on at least 3 factors. First, the environment must be within the physiologic niche of the species. A species range on disturbed sites across the broad altitudinal gradient suggests the breadth of the physiologic niche. Second, the environment/vegetation must be within the realized niche of the species. Presence in undisturbed vegetation of an environmental type demonstrates presence in the realized niche, with respect to climax (= late seral) vegetation. And third, presence in either disturbed or undisturbed sites demonstrates that the species has dispersed to the site. While proximity to a highway maximized the exotic's likelihood of arrival at the sites we studied, sites in environmental types in the agricultural zone had far more exposure to invading propagules than did sites in the high mountains.

On disturbed sites the exotic richness (species number) across the environmental gradient seems remarkably constant (Fig. 1), despite changes in its composition (Table 3). Regulars (constancy >30%) were 8–12 except in shrublands (5–7), one conifer forest (7), mountain meadows (5), and tundra (1). While one might argue that incidentals (constancy <30%) indicate microsite effects, numbers of incidentals were also rather constant (2–6), except in the *Pseudotsuga/Symphoricarpos* environment (11). Thus, disturbed sites seem to have a more or less constant "richness capacity," but filled with species differing among environments. Shrubland environments are slightly species deficient, for no obvious reason. *Pseudotsuga* environments have a small excess, possibly due to their location at elevations supporting floras from Mediterranean/steppe environments and northern coniferous environments. While we see no corresponding break in environmental rigor (Table 2), the tundra environment is notably exotic poor.

In contrast, numbers of species invading undisturbed vegetation of different environmental types vary greatly (Table 3): grasslands (7–13), aspen (8), dry *Pseudotsuga* forests (8–10), other conifer forests (0), and alpine (2). This suggests that the undisturbed vegetation of major environmental types differs greatly in competitiveness. In grasslands and dry forests, exotics occupying disturbed sites, i.e., tolerating the physical environments, also colonize adjacent undisturbed vegetation. The open structure of these vegetation types apparently provides noncompetitive microsites for these exotics. The exotic deficiency seen in the shrub zone was also seen on disturbed sites and is most likely induced by the physical environment. In contrast, exotics known to tolerate physical conditions in the conifer zone (i.e., disturbed sites) rarely invade adjacent forest. These exotics are probably excluded from forests by heavy competition for water/nutrients (Watt and Fraser 1933) or light. Thus, removal of forest communities, by fire or harvest, should allow plants capable of occupying noncompetitive disturbed sites to colonize more widely in the forest environment, where they may inhibit forest establishment but will finally yield when they are overtopped by tree species.

The low exotic richness of the alpine is probably due in part to environments too rigorous for establishment of opportunists (Billings and Mooney 1968), but this does not explain the sharp decline from the forest and meadows below. It is likely that failure of dispersal also contributes. To illustrate, we contrast the exotic presence in alpine and mountain meadow vegetation. (1) First, while plants adapted to disturbed Old World alpine environments may exist, vectors—crops, animals, machinery—rarely pass directly from these areas to high-altitude areas in the Rockies. Thus, the transfer of potential weeds has been slight. We conservatively suggest that as recreational use grows, managers should minimize introductions (exchanges) of exotics by increasing both quarantine and efforts to detect and eradicate unwanted establishment. (The presumed need for this caution might be tested by showing that alpine opportunists are available in the Old World [Alps, Himalayas, Southeast Asia] flora and that the grazing disturbance has been sufficient and environmental rigor slight enough to induce the evolution of opportunistic species.) (2) In contrast, while mountain meadows seem almost equally isolated, our culture has provided a stepping stone for exotics to them. The exotics have been introduced to environmentally similar foothill sites through commercial and agricultural activity, have established, and are being transported upward, especially as motorized backcountry use increases. For example, while an experimentally bared portion of a remote mountain meadow (Weaver and Collins 1977) was not infected by *Cirsium arvense* in the preceding 2 decades, thistle appeared soon after loggers entered nearby forests.

Distribution of Individual Species

Knowledge of the tolerance range of a species tells us where to look for established stands and where to expect establishment. Both are useful in planning control. It may also help us estimate a species' ability to cross stressful—dry or cold—zones without assistance. The importance of the latter is declining as human transport becomes the dominant dispersal mechanism.

DISTRIBUTION AMONG DISTURBED SITES.—The physiologic niche of a species is suggested by its presence in disturbed sites because open spacing reduces competition. We recognize 4 distribution types (niche types).

First, species with narrow distributions are most important in lower, warmer environments (Table 3). Some occupy dry grasslands (*Agropyron cristatum, Alyssum alyssoides, Camelina microcarpa,* and *Bromus japonicus*), shrublands (*Rumex acetosa*), and warm forests (*Dactylis glomerata, Festuca pratensis, Verbascum thapsus*). None are important in the moist conifer zone, cool conifer zone, or mountain grasslands/tundra. In our data *Chrysanthemum leucanthemum* seems to have narrow tolerances, but it is spreading rapidly into drier environmental types including those dominated by *Pseudotsuga menziesii* and *Festuca idahoensis.*

Second, plants with broader tolerances populate wider zones in the altitudinal gradient (Table 3). Low-site plants (*Tragopogon dubius, Centaurea maculosa,* and *Melilotus officinalis*) may prefer grasslands over shrublands. Exotics dominating near the lower forest margin plants include *Cirsium arvense, Poa compressa,* and the most drought tolerant (?) of the clovers (*Trifolium procumbens*). *Trifolium pratense* occurs throughout the low/warm conifer zone. *Trifolium repens, T. hybridum,* and *Agrostis alba* occur in the moist conifer zone, both low/warm and high/cool.

Third, 2 plants (*Poa pratensis* and *Taraxacum officinale*) have remarkably wide distributions, extending from low grasslands through forests to mountain meadows and even tundra (Table 3). Two others (*Bromus inermis* and *Phleum pratense*) range from moister grassland environments through forest environments to mountain meadow environments. All of these species cover 2–5% (D in Table 3) or 5–25% (E) of the ground surface on disturbed sites in some environments they occupy.

Fourth, 5–6 species representing 2 subgroups have interrupted or bimodal distributions (Table 3). First, *Lactuca serriola* and *Bromus tectorum* were found in dry grasslands (*Bouteloua* and *Agropyron*), were absent from moister grassland environments, and reappeared in dry forests (*Pseudotsuga*). One might speculate that these species tolerate arid environments, cannot compete in moister grassland environments, and become competitive again where precipitation evaporates from treetops before it becomes available to plants in the ground layer. This hypothesis would be more convincing if the interruption occurred in the undisturbed zone, but not in the disturbed zone. The same interruption was reported for 2 native grasses (*Stipa viridula* and *Koeleria nitida*) and 5–10 exotic species (including *Bromus inermis, B. tectorum, B. japonicus,* 3 annual mustards, and *Kochia scoparia*) that are present in the dry plains of eastern Montana, disappear in the foothills and grasslands, and reappear in the *Pseudotsuga* zone to the west (Weaver and Meier 1997). Second, 3–4 species have modes in both a lower-elevation zone and in the *Abies*/mountain meadow zone. *Descurania* (listed as unimodal) appears in dry grasslands and has a weak high mode. *Polygonum* and *Madia* appear first in moister grasslands and have solid high modes. *Medicago* appears first in the dry forest zone (*Pseudotsuga*) and reappears in the *Abies*/mountain meadow zone. We speculate (hypothesize) that plants of the lower mode occupy a site dry due to lack of precipitation and those of the high mode occupy sites dry due to the high wind flows near mountain ridges (cf. Weaver 2001).

Each altitudinal zone contains species of both narrow and broad environmental amplitudes. This is demonstrated by listing the species within an amplitude group according to their locations on the altitudinal gradient (Table 3). Thus, among species with narrow distribution, *Agropyron cristatum,* important only in the driest environments, appears first. And among species with broad distribution, *Poa pratensis* appears before *Taraxacum officinale* because it becomes important at lower altitudes.

DISTRIBUTION AMONG UNDISTURBED SITES.—The tendency of exotics to escape from distribution corridors is inversely related to the penetrability of adjacent vegetation. Thus, while establishment on disturbed sites provides an indication of the physiologic niche, invasion of natural vegetation provides an indication of the realized niche, i.e., performance under competition from natural vegetation.

The escape of species of all amplitudes and gradient segments is proportional to the openness of the adjacent native vegetation. Species of narrow to moderate altitudinal ranges often escape into relatively open grassland or Douglas-fir (*Pseudotsuga*) vegetation, but they are unlikely to escape into denser subalpine fir forests (*Abies;* Table 3). Similarly, species with broad ranges tend to escape into grassland and low forests but are unlikely to escape into dense forest environments (Table 3). Given these observations, we expect bimodal species to escape in their lower, drought-stressed environments, but to be competitively constrained in their upper, moister environments. This is true except where the environment in the upper arm is sufficiently wind-dried to create competitive conditions (and escape) similar to that in the low-elevation mode (Table 3). *Polygonum aviculare* and *Madia glomerata* are bimodal plants illustrating the last point.

While undisturbed vegetation in the center of the forest zone may be impenetrable, segments of the forest zone that have been logged or burned are probably more penetrable, either because competition for light or water/nutrients (Watt and Fraser 1933) is reduced or because wind dispersal is facilitated. Analysis of comparable samples (existing data) will eventually test this hypothesis.

TABLE 4. Median constancy of both invading species and noninvading species on disturbed sites. The lower constancy of noninvading species may indicate poorer adaptation or a smaller seed supply.

Environmental type (HT)	BOGR STCO	AGSP BOGR	FEID ARAR	FEID ARTR	FESC FEID	PSME SYAL	PSME PHMA	POTR CARU	FEID AGCA	DECA CARX	Over-all
Invaders	5.0	5.0	7.0	5.0	6.0	5.0	5.0	7.5	2.0	1.0	5.0
Noninvaders	1.5	1.0	1.5	2.5	2.5	1.0	5.0	2.5	2.0	0.0	1.0
$P = 0.0005$[a]		0.07	0.23	0.08	0.16	0.06	0.06	0.61	0.06	—	0.57

[a] Kruskal-Wallis test (Gibbons 1985)

We expect the dominance of a species on disturbed sites of an environmental type to indicate its capacity to invade undisturbed sites in that environmental type, both because a species thriving on the disturbed site must be well adapted to the physical environment it occupies and because, as a well-adapted species, it will produce more seed. Our hypothesis is, then, that invading species will be more dominant on adjacent disturbed sites than noninvaders. In fact, the median constancy of invaders usually does exceed the median constancy of noninvaders, and the difference is significant in 70% of the cases (Table 4). When data are pooled across all except the moist conifer types, which show no escape, the difference is significant ($P < 0.0005$). The moist conifer types, PSME/PHMA, TSHE, and ABLA forests are reasonably excluded from this analysis because no exotic species have moved from roadside to forested environments.

Evaluating Exotics

If public forest and park vegetation is to be managed for "pre-Columbian" condition (cf. U.S. Congress 1872), exotics should be excluded. If this is impossible, managers should strive to prevent exotics from dominating the vegetation because dominants are most likely to affect the success of native plant associates and, through their influence on vegetation composition, animal associates as well (cf. Clinton 1999). In evaluating species, we minimize "breadth of distribution" as a criterion on the assumption that conservationists should equally emphasize preservation of all vegetation types important in the region. Vegetation types rare in the region deserve special attention if they are endemic to it, but they are less critical if they are well represented in other regions. Because our project was designed for generality, we studied no rare types.

Sites undergoing primary succession are rare in the forest and grassland zones (e.g., river deposits or landslides) and more common in ridge sites of the alpine (e.g., undecomposed rock). Although slopes of our roadside sites may be steeper than the average disturbed site, our data (Table 3, cover classes D and E) probably identify the most problematic species of upland sites undergoing primary succession. On disturbed grassland sites (including mountain meadows) the only exotic with 5–25% cover (E) was *Poa pratensis* and exotics having 2–5% cover (D) were *Bromus inermis, B. tectorum, Phleum pratense,* and *Rumex acetosa.* In dry forests exotics with cover 5–25% (E) were *Dactylis glomerata* and *Phleum pratense,* while those with cover 2–5% (D) were *Agrostis alba, Bromus inermis,* and *Trifolium repens.* In moister conifer forests, those with cover 5–25% (E) were *Bromus inermis, Melilotus officinalis, Taraxacum officinale,* and *Trifolium hybridum*; and 2–5% (D) were *Medicago lupulina, Phleum pratense, Trifolium pratense,* and *T. procumbens.* No exotic covered as much as 5% of either disturbed or undisturbed sites in the alpine. Ironically, the most aggressive exotics are rarely discussed as problematic, and none of the exotics designated as noxious seem to dominate in the wide range of environments we studied.

Secondary secession sites—such as recent burns, logged areas, or old fields—are more common on public lands than are primary succession sites. Here, the performance of exotics may be similar to their performance on primary succession sites. This expectation may overstate the problem since exotics, mostly dispersing laterally through space, must compete with natives colonizing both from the propagule bank and dispersing laterally. Thus, we expect the grasses (*Agrostis, Bromus, Dactylis, Phleum,* and *Poa*), legumes (*Melilotus, Medicago,* and *Trifolium*), and dandelion, listed above, to be among the most important exotic invaders.

Late seral sites may be as common as or more common than secondary succession sites in national forests and parks. Later seral vegetation of moister forests is impenetrable, but grasslands, shrublands, and dry forests are invaded by many species (Table 3). However, because dominance of all species falls from disturbed to undisturbed sites, we discount most of the species not listed as invaders of secondary succession sites. This position may understate the effects of robust (e.g., *Agropyron cristatum* or *Melilotus officinalis*) or very numerous (e.g., *Bromus tectorum, B. japonicus,* or *Alyssum alyssoides*) plants of the driest environmental types.

CONCLUSIONS

The number of exotics currently common in vegetation of the northern Rocky Mountains is relatively few, approximately 29 (Table 3). The altitudinal (temperature/moisture) amplitude of each of these species is described by presence in environmental types (HTs) representing segments of the environmental gradient (Table 3). Knowledge of species amplitudes will enable managers to estimate and even map potential distributions of exotics, both in disturbed (primary succession) and undisturbed (late seral) vegetation.

The overall invasibility of major environmental types—in both disturbed and undisturbed conditions—is indexed by tabulating exotic species richness across a broad altitudinal gradient of types. Grasslands and dry forest environments harbor the most exotic species, both in disturbed and undisturbed sites. Moist conifer forests have similar species richness on disturbed sites, but no exotics appear on undisturbed sites. Tundra environments support few exotics on either disturbed or undisturbed sites.

Dominance in vegetation in at least one environmental type is our criterion for recognizing an exotic of special concern, because a dominant is most likely to affect the success of plant associates and, through its influence on vegetation composition, the success of animal associates as well. We minimize breadth of distribution as a criterion on the assumption that conservationists should emphasize equally the preservation of all regionally common and internationally unique ecosystems. Seven species exhibited cover of 5–25% on disturbed sites they occupied in at least one type (Table 3); they include grasses (*Agrostis, Bromus, Dactylis, Phleum,* and *Poa*), legumes (*Melilotus, Medicago,* and *Trifolium*), *Rumex* and *Taraxacum* species. An additional seven species exhibited cover of 2–5% on disturbed sites in at least one environmental type (HT). Most of these plants were introduced intentionally and none of these stealth plants is normally considered a noxious weed.

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Site and stand characteristics related to white pine blister rust in high-elevation forests of southern Idaho and western Wyoming

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SITE AND STAND CHARACTERISTICS RELATED TO WHITE PINE BLISTER RUST IN HIGH-ELEVATION FORESTS OF SOUTHERN IDAHO AND WESTERN WYOMING[1]

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ABSTRACT.—Successful infection of white pine species by white pine blister rust (WPBR) is contingent upon environmental conditions that are favorable to the spread and development of *Cronartium ribicola.* Site and stand factors related to this process have been studied elsewhere within the distribution of the disease, but few studies have concentrated on the high-elevation white pine forests of southern Idaho and western Wyoming. We found that mean summer precipitation, average tree diameter, and elevation were the most important variables in 3 logistic regression models of WPBR presence and intensity. The models were tested on a randomly chosen portion of our data set. The model with 9 variables correctly predicted categories of low-, moderate-, and high-disease incidence in 79% of cases. The 2 models with fewer variables had lower predictive efficiencies but were more parsimonious and generally easy to measure. The ability to use easily measured or remotely sensed site and stand characteristics to predict WPBR spread or intensification could be an important asset to land managers who need to decide where to focus disease mitigation efforts and predict disease effects on water quality, wildlife habitat, recreation potential, and other land-management activities.

Key words: white pine, whitebark pine, limber pine, white pine blister rust, Cronartium ribicola, *tree diseases, Rocky Mountain forests, subalpine forests.*

White pine blister rust disease (WPBR), caused by the introduced fungus *Cronartium ribicola,* is the most widespread and serious disease of *Pinus albicaulis* (whitebark pine; Arno and Hoff 1989) and *P. flexilis* (limber pine) in the Rocky Mountains (Smith and Hoffman 2000). The disease is also a potential threat to most, if not all, other white pine species (genus *Pinus*, subgenus *Strobus,* section Strobus, subsections Cembrae and Strobi, and section Parrya, subsection Balfourianae; Hoff et al. 1980). The rust causes branch and stem cankers that, in most cases, girdle and kill the host tree.

Cronartium ribicola has a complex life cycle that is characterized by 5 spore-producing stages that alternate infection between white pine species and plants of the genus *Ribes* (currants and gooseberries). Aeciospores are small, light spores that are produced on pine cankers and can travel long distances to infect the leaves of *Ribes.* Urediniospores emerge on *Ribes* leaves and spread to other leaves on the same plant, or other nearby *Ribes* plants. Teliospores, produced on *Ribes,* germinate and form the basidium, which releases basidiospores to infect white pine needles. Fungal hyphae spread into woody tissue causing cankers, where the 5th type of spore-bearing structure, the pycnium, is produced. Upon completion of the pycnial stage, which probably involves mating, aecia are produced, completing the life cycle.

Like other pine rusts, transmission of spores and host infection depends on a favorable temperature and moisture environment, an abundance of spores (inoculum), and availability of susceptible hosts (Mielke 1943, Charlton 1963). These conditions may be affected by physical factors such as slope, aspect, elevation, and precipitation, as well as biological factors such as structure of the forest canopy and proximity of *Ribes* spp.

Site and stand factors associated with rust incidence have been identified by studying the distribution of WPBR and endemic pine rusts. Van Arsdel (1972) found that the size of forest canopy openings and certain topographic features were related to WPBR incidence in *Pinus strobus* (eastern white pine). In British Columbia, Hunt (1983) reported more WPBR

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cankers in *P. monticola* (over 2.5 m high in the tree) as slope increased. Jacobi et al. (1993) found *Cronartium comandrae* (comandra blister rust) incidence in *Pinus contorta* subsp. *latifolia* (lodgepole pine) positively correlated with tree diameter, and negatively correlated with stand density and distance to the rust's telial host. Beard et al. (1983) found a greater incidence of *C. coleosporioides* (stalactiform blister rust) in central Idaho *Pinus contorta* forests at middle to upper elevations, and in *Abies lasiocarpa/Xerophyllum tenax* and *Abies lasiocarpa/Vaccinium scoparium* habitat types. *Endocronartium* (=*Peridermium*) *harknessii* (western gall rust) stem infections were negatively correlated with stand age in British Columbia *Pinus contorta* forests (van der Kamp 1988). Van Arsdel (1965) constructed a formula based on slope and canopy openings and predicted WPBR presence in southwestern Wisconsin with 89% accuracy. Charlton (1963) used aspect, elevation, slope, topographic position, and vegetation structure, along with climatic factors, to assess WPBR infection hazard in the eastern U.S. A comprehensive site-specific WPBR hazard model based on site, stand, alternate host, and physiological factors was developed by McDonald et al. (1981) for *P. monticola* in northern Idaho.

Very little of this type of work has been conducted in the southern portion of *C. ribicola*'s range in the Rocky Mountains because, historically, disease surveys revealed only trace levels of infection (Brown 1967, Brown and Graham 1969). However, WPBR has recently intensified and spread to new locations in the southern portions of the Northern Rocky Mountain and Middle Rocky Mountain provinces (Kendall et al. 1996, Smith and Hoffman 2000). As an initial step in modeling WPBR spread and intensification in this region, we used USDA Forest Service disease survey data (Smith and Hoffman 1998) to look for relationships between WPBR incidence and several site and stand characteristics.

STUDY AREA

Pinus albicaulis and *P. flexilis* populations in the U.S. extend southward along the Rocky Mountains from the Canadian border to southeastern Idaho and southwestern Wyoming. *Pinus flexilis* extends even further south, throughout the mountains of Utah. There are also several disjunct *P. flexilis* and *P. albicaulis* populations in isolated mountain ranges of eastern Oregon and northern Nevada, and both species occur in the Sierra Nevada (Critchfield and Little 1966). Our study area encompasses those Rocky Mountain white pine populations that lie within southern Idaho and western Wyoming (Fig. 1). Within this region *P. albicaulis* and *P. flexilis* populations extend upward from the lower subalpine zone to the upper (cold) tree line. *Pinus flexilis* also has the unique ability to grow at lower (dry) tree line (Arno and Hammerly 1984).

FIELD METHODS

In 1995 we installed 10 rectangular plots according to the methods specified by the Whitebark Pine Monitoring Network (Kendall 1995). In 1996 we used randomly located strip transects rather than rectangular plots to delineate trees. We switched to transects because white pine species in our study area tend to grow as dispersed woodlands or as infrequent seral components in subalpine forests. Obtaining 50 white pines in a rectangular plot of a reasonable size was often not possible. For the 68 sites sampled during 1996, we established a 4.6-m (15-ft)-wide strip transect, along the contour of the slope, from a random starting point. We traversed this transect until 50 white pines had been inspected or until we encountered a change in the character of the site or stand that did not match our sampling criteria, such as a different canopy structure, a sufficiently different aspect (>10° difference), slope (>5% difference), habitat type or phase, or a topographic change. Rather than cross this environmental gradient, we changed the direction of the transect by 180°, displaced it uphill or downhill 4.6 m (15 ft), and continued to sample until 50 trees had been inspected.

For each tree we recorded the presence of WPBR cankers and DBH (diameter at breast height, 1.37 m above the ground), in 5.1-cm (2-in) size classes. At the midpoint of each transect, we measured or calculated habitat type (Steele et al. 1981, 1983), presence/absence of *Ribes* sp., basal area, trees per hectare, canopy closure, elevation, aspect, slope angle, and topographic position (Table 1).

An additional variable, estimated mean summer precipitation, was generated from climate maps (Martner 1986, Molnau and Newton

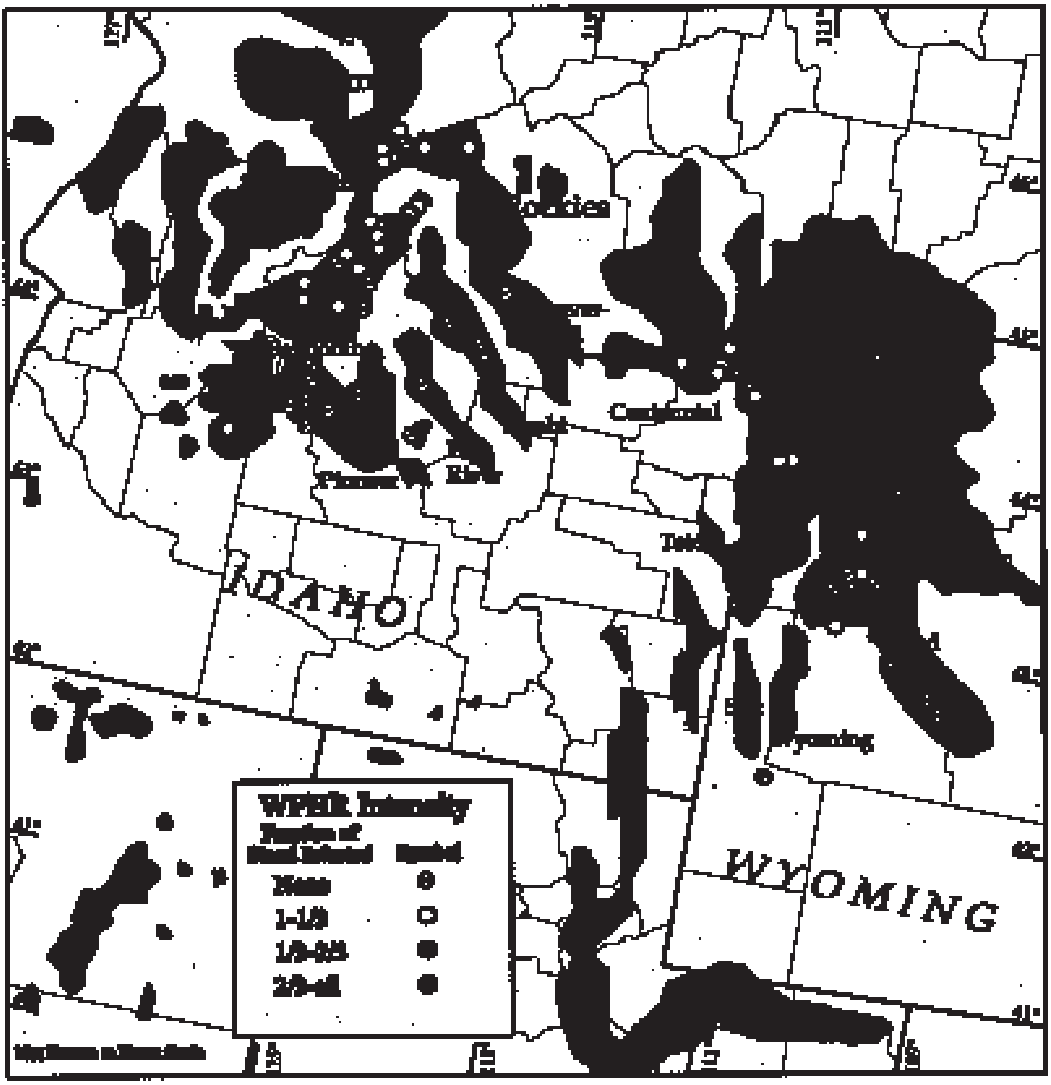

Fig. 1. Northern and middle Rocky Mountain ranges, sample locations, and white pine blister rust intensity for 78 sample sites inspected in 1995–1996. Distribution of white pine species (shaded areas) derived from Little (1971).

1994). To estimate mean summer precipitation, we multiplied regionalized estimates of the summer (June, July, and August) proportion of total precipitation by the mean annual precipitation values taken from these maps. We interpolated precipitation values between isohyetal contours for each of our sample sites.

STATISTICAL METHODS

Because sampling location criteria and data collection procedures were identical for plots and transects, the data were combined for our analysis. We grouped the categorical independent variables, habitat type, canopy cover, and topography to reduce the number of categories for model calculation. For example, we identified 20 habitat type classes in the field but combined these into 4 categories based on a multidimensional scaling procedure that groups habitat series based on moisture requirements of understory plants (McDonald unpublished data). We used dummy coding for the categorical variables. Presence or absence of *Ribes* spp. was entered as a binary variable (i.e., a value of 0 for absent, 1 for present).

TABLE 1. Variables used in the stepwise logistic regression procedure and parameter estimates for the 3 models using the recombined (full) data set.

	Standardized parameter estimate (Wald χ^2)		
Variable (description)	Model 1	Model 2	Model 3
Elevation (meters, from topo map)	–0.613 (313)	–0.606 (321)	–0.546 (308)
Average DBH (diameter at breast height in 2-cm classes)	0.458 (212)	0.454 (210)	0.517 (301)
Mean summer precipitation (interpolated from maps)	0.278 (109)	0.304 (145)	0.250 (111)
Ribes (present/absent in stand)	0.237 (62)	0.239 (69)	
Stand density (trees · ha^{-1}, all species)	–0.258 (61)	–0.222 (55)	
Topographic position 3 (upper slopes)	0.215 (56)	0.212 (55)	
Habitat type 1 (wet subalpine fir group)	0.123 (28)		
Slope (percent)	–0.109 (12)	–0.118 (15)	
Habitat type 4 (whitebark pine series)	0.007 (7)		
Basal area ($m^2 \cdot ha^{-1}$, all species, white pines only)			
Aspect (cosine of aspect in degrees)			
Latitude (UTM–northing)			
Canopy (open, broken, closed)			
Topography (valley/lower, mid, upper, ridge)			
Habitat type (wet subalpine fir, cool/moist subalpine fir, cold/dry subalpine fir, whitebark series, Douglas-fir)			

Elevation, slope, latitude (UTM northing), average tree size, and mean summer precipitation were entered as continuous variables (i.e., their actual measured values). The aspect measurement, which is azimuthal (circular data), was linearized by taking the cosine of the aspect in radians.

Logistic Regression Analysis

Percent of trees infected in a sample stand was the dependent variable, which was treated statistically as the number of successful events (infected trees) per number of trials (trees sampled) at each sample site. We performed a stepwise logistic regression procedure with the model development data set using the PROC LOGISTIC STEPWISE option in SAS (SAS Institute Inc. 1996). This procedure identifies predictive variables when the number of potential explanatory variables is large relative to the number of samples (Hosmer and Lemeshow 1989). We constructed 3 models of WPBR incidence with combinations of the variables selected by the stepwise procedure.

To determine if models were statistically significant, we compared 4 criteria to assess how well the models fit and to compare how well each model predicted WPBR incidence. First, we calculated r^2_L, which is a measure of the reduction in the log-likelihood as a result of including the independent variables (Menard 1995). We tested the null hypothesis that the predictor variables contribute no more than chance to the explanation of the dependent variable with the G_m statistic (the model chi-square statistic). The Bayesian information criterion (BIC) was calculated as a selection device because it emphasizes parsimony by penalizing models with a large number of parameters (Ramsey and Schafer 1997). To measure the predictive efficiency of each model, we arbitrarily assigned broad classes of WPBR incidence, low (<25% incidence), medium (26–50%), and high (>50%), to the observed and predicted values and then calculated how frequently each model correctly predicted the observed category, was 1 category off, or was off by 2 categories.

Model Testing

We used a split-sample validation technique to develop and test the logistic regression models. Each record was assigned a random number, sorted by this number, and then split into a model-development data set (2/3 of the data), which was used to develop the models. The remaining 1/3 of the data ($n = 23$) was treated as an independent data set to test the models' statistical significance, fit, and predictive efficiency, and to assess the importance of the independent variables. We estimated the predicted proportion of trees infected in each sample with the predicted probability of infection (presence or absence of WPBR) for each tree in that sample.

Table 2. Fit statistics and prediction efficiency for 3 logistic regression models of WPBR incidence using the model-developing data set (A) and the model-validation data set (B).

A								Prediction of incidence category				
Model	χ's	G_M[a]	P[b]	R^2[c]	R^2_L[d]	BIC[e]	n[f]	Correct	Under 1	Over 1	Under 2	Over 2
1	9	502	0.001	0.483	0.179	2326	49	37(76%)	3	5	2	2
2	7	487	0.001	0.473	0.173	2339	49	37(76%)	5	4	2	1
3	3	370	0.001	0.347	0.129	2502	50	33(66%)	8	7	2	0

B					Prediction of incidence category				
Model	χ's	P[b]	R^2[c]	n[f]	Correct	Under 1	Over 1	Under 2	Over 2
1	9	0.001	0.448	24	19(79%)	3	1	1	0
2	7	0.001	0.384	24	18(75%)	3	2	1	0
3	3	0.001	0.405	24	15(62%)	6	3	0	0

[a] Model chi-square
[b] Statistical significance of model
[c] Coefficient of determination
[d] Reduction in log-likelihood due to the model
[e] Bayesian information criterion
[f] Number of observations; differences due to missing values for some variables

The probability of WPBR infection in a tree [P(Y)] was obtained by inserting the test data independent variables into the equation for each model. The equations calculated logit(Y) (the natural logarithm of the odds of WPBR infection) rather than P(Y) directly. The form of the equation was

$$\text{logit(Y)} = \hat{\beta}_0 + \hat{\beta}_1 \times x_1 + \hat{\beta}_2 \times \hat{\beta} x_2 + \ldots\ldots + \hat{\beta}_k \times x_\mathrm{k},$$

where logit(Y) = ln {P(Y)/[1 – P(Y)]}, $\hat{\beta}_0$ is the Y-intercept, x_1 through x_k are the independent variables identified by the stepwise procedure as important predictors of WPBR incidence, and $\hat{\beta}_1$ through $\hat{\beta}_k$ are the coefficients for these independent variables. It was necessary to linearize the predicted value to compare it to the linear observed proportion of trees infected. To accomplish this, logit(Y) was converted to odds(Y) by exponentiation, and then to P(Y) by the formula P(Y) = odds(Y)/[1 + odds(Y)], where P(Y) is the predicted probability of infection in an individual tree and odds(Y) is the ratio of the probability that Y = 1 to the probability that $Y \neq 1$.

We used least-squares regression to compare the predicted proportion of trees infected with our observed proportion of infected trees and to calculate the significance of the regression and the coefficient of determination. Finally, we assigned the low, medium, and high classes to the predicted and observed values and performed a simple error assessment to see how well the model predicted incidence.

Analysis of the Independent Variables in the Model

To assess the importance of the independent variables, we evaluated the odds ratio, which approximates how much more likely the event (WPBR presence in a tree) becomes with increases or decreases in the value of each independent variable (SAS 1996). We also used the standardized logistic regression coefficients to evaluate the strength of the relationship between each independent variable and the dependent variable (Menard 1995).

Results

Model Development and Validation

The stepwise logistic regression identified 13 variables that were potentially related to WPBR infection. We used these to develop 3 candidate models. For the 1st model we removed 4 variables that were highly correlated ($r > 0.6$) or that were not significant ($P > 0.05$). We created the 2nd model by removing the variables with Wald-χ^2 values <20. The 3rd model contained only the 3 variables that stood apart from the others because of their very high Wald-χ^2 values (>100). Fit statistics, significance, and predictive efficiency for the 3 models are shown in Table 2A.

When applied to the validation set, all 3 regression models were statistically significant ($P \leq 0.001$). The coefficient of determination (r^2) for the models ranged from 0.38 to 0.45.

The level of classification accuracy was highest for model 1, which correctly classified 79.2% of the cases. Model 3 correctly classified 62.5% of the test cases and had a higher r^2 than model 2 (Table 2B).

Importance of Independent Variables in the Model

The most important variables in all 3 models were elevation, mean summer precipitation, and average DBH. Although other variables were also statistically significant, when combined, these variables accounted for a much smaller proportion of the variation in WPBR incidence than the first 3 variables. Table 1 lists the parameter estimates for the variables in each model.

DISCUSSION

Interpretation of Independent Variable Selection

ELEVATION.—In Yellowstone National Park, Berg et al. (1975) reported that WPBR incidence in *Pinus albicaulis* and *Pinus flexilis* decreased with elevation. These researchers found that 92% of all infections occurred below 2591 m (8500 ft) elevation. Our results suggest a similar negative relationship between elevation and WPBR incidence. We found that 97% of the sample stands below 2591 m had WPBR, while only 53% of the stands above 2591 m were infected. However, the average proportion of trees infected in these stands did not decrease with elevation. In fact, the proportion of high-infection sites above 2591 m, 33%, was slightly greater than the proportion of high-infection sites below this elevation, 31%, suggesting that once WPBR is able to infect a high-elevation site, it is able to continue to intensify. However, this phenomenon was apparent only in the Greater Yellowstone Ecosystem portion of our study area. Some factors involved in the decrease in WPBR incidence with increasing elevation may include earlier *Ribes* leaf senescence, cooler temperatures at key times of development or spore dispersal, less susceptible *Ribes* species, or a less favorable spatial pattern of hosts at higher elevations.

PRECIPITATION.—Mean summer precipitation was an important predictor variable in our model. Other researchers have observed a relationship between WPBR incidence and regional moisture characteristics. For example, Van Arsdel et al. (1956) attributed low WPBR incidence in southwestern Wisconsin to the dry climate of the region.

Optimal temperature and moisture conditions for survival of *Cronartium ribicola* have been well documented (Mielke 1943, Van Arsdel et al. 1956). Infection of pines requires extended periods of time (Charlton 1963) during late summer and early autumn with nighttime temperatures below 19.4°C (67°F) and free moisture on the needle surfaces (Kimmey and Wagener 1961). Van Arsdel et al. (1956) concluded that at least 2 consecutive days of these favorable conditions are required for infection of pines.

Extended temperature data from high-elevation weather stations within our study area were not available, and interpolating temperatures between low-elevation weather stations is inappropriate because of local temperature inversions that are common in mountain environments (Baker 1944). Thus, we did not include a temperature variable in our analysis. We were also unable to locate climate data for mountainous areas that included summer moisture estimates other than mean precipitation amounts. It is generally thought that moist summers are conducive to WPBR development and spread; however, mean summer precipitation alone is probably not the best indicator of favorable climate conditions. For example, Mielke (1943) noted that a heavy “flare up” of WPBR incidence occurred in Idaho during a summer of relatively low mean precipitation in 1937. In fact, dew may be an equally important source of moisture (Mielke 1943). Cloudy summer periods and high relative humidity periods may be better indicators of WPBR incidence than precipitation.

AVERAGE TREE DIAMETER.—The importance of average tree diameter at breast height (DBH) in the logistic regression model may be due to 2 factors. First, smaller-diameter trees tend to have less foliage than larger-diameter trees and are therefore smaller targets for spores. Second, most cankers we inspected were in the upper portion of tree crowns in the interior of stands or throughout the crown of trees on an open edge of the stand. We speculate that wind patterns during times of basidiospore dispersal from *Ribes* to pines concentrate infections along the windward and upper sides of a stand. Wind-dampening effects of the forest canopy and screening of spores by larger trees may reduce the transfer of spores to smaller, more sheltered trees.

While diameter could reflect the length of exposure, the length of exposure is probably not important because even the smallest trees in our samples likely pre-date WPBR presence in the region.

Average DBH appears to be more important to the intensity of infection on sites that are infected than to WPBR incidence. Of 16 stands with an average DBH of <10 cm, all but 2 were infected, with an average infection level of 19.5% (2–85%) for the infected stands. Of 14 stands with ≥20 cm average DBH, 4 were uninfected, and the average infection rate for the infected stands was 46.3% (2–87%).

OTHER VARIABLES.—Other variables were statistically significant in the stepwise logistic regression analysis. However, these variables had much lower Wald-χ^2 values and contributed proportionally much less to explaining observed variability in incidence than elevation, mean summer precipitation, and average tree diameter. Due to the low Wald-χ^2 values and potential correlations between these variables, their statistical and biological significance is suspect. Also, since we did not test each of the independent variables, it is possible that we included irrelevant variables in the model.

Implications for Future Research

The potential relationships between site and stand characteristics that we identified in this analysis represent a "snapshot" in time for the current stage of the developing WPBR epidemic in our study area. These relationships help identify areas where WPBR will likely spread and/or intensify first. Aging cankers could help researchers (1) determine how WPBR has moved and intensified in the region and (2) differentiate between sites susceptible to long-range transmission and those where WPBR intensifies quickly. Such a study could also help researchers predict future spread and intensification of WPBR in the region. However, the characteristics of spread and intensification may change in the future due to genetic adaptations by *Cronartium ribicola*, an exponential increase in inoculum availability, changes in host distributions, or shifts in regional climate patterns.

Management Implications

The ability to identify areas of potential rapid intensification or areas with a low probability of infection or intensification over time would help land managers direct mitigation efforts. For example, a spatial model that identifies these areas of intensification could aid the ongoing search for phenotypically resistant trees, which are highly visible in severely infected stands. In some areas vegetative competition from *Abies lasiocarpa* (subalpine fir) is as much of a concern as WPBR (Keane et al. 1994). A spatio-temporal WPBR spread and intensification model would help managers decide where treatments to reduce this competition would be effective. Where WPBR intensification probability is low, silviculture and/or prescribed fire could be used to reduce competition and provide regeneration opportunities for white pines. Conversely, conducting these activities in areas with a high probability of WPBR intensification could potentially increase inoculum levels through the regeneration of susceptible white pines or an inadvertent increase in *Ribes* abundance. A predictive model could also help resource planners assess the future effects of white pine mortality on wildlife, water quality and quantity, avalanche activity, and recreation.

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Invisible invasion: potential contamination of Yellowstone hot springs by human activity

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INVISIBLE INVASION: POTENTIAL CONTAMINATION OF YELLOWSTONE HOT SPRINGS BY HUMAN ACTIVITY[1]

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ABSTRACT.—This report establishes a baseline inventory of microorganisms in acidic hot springs of Yellowstone National Park (YNP). The analysis is based on observations carried out over the past 25 years using light microscopy, DNA staining, and electron microscopy of environmental samples. The inventory, while incomplete in that not all organisms have been cultured or examined using genetic approaches, represents a study of several solfatara (acid sulfate) geyser basins in YNP. We found that the types of microorganisms in flowing springs had changed over time. In contrast, no such changes occurred in mixing pools. We solicited opinions of prominent YNP microbiologists to address the issue of change in the context of human cross-contamination of springs and to suggest sampling protocols. While the consensus is that research has not introduced exotic species, this explanation is always uncertain. The issues related to this uncertainty, including human cross-contamination, are discussed, and sampling methods designed to best preserve the springs for future investigations are described.

Key words: hot spring, sulfur, acid, contamination, microorganism, microbe, Yellowstone National Park.

Discovery of life at high temperature (Brock 1978) led to advances in biotechnology made possible by *Thermus aquaticus* (Taq), which was isolated in Yellowstone National Park (YNP; Brock and Freeze 1969). Since Taq polymerase chain reaction (PCR) became a patented process for in vitro amplification of DNA, PCR has generated significant scientific advances in biotechnology and substantial revenues (Brock 1994) for the patent holder. The commercial success of *T. aquaticus* led to an increase in collection activity and research in the Yellowstone geothermal ecosystem. Scientists seeking other utilitarian, heat-stable enzymes in the protected, mostly unexplored hot spring habitats generated dozens of research permits in the 1990s, allowing microbial exploration in YNP.

Only a small number of organisms from the hot springs in YNP have been isolated (Lindstrom 1997). As a result, there is no existing microbial inventory to evaluate whether investigators who visit a series of springs inadvertently introduce exotic microbes via sampling equipment or mud carried from one spring to another. Hence, without a historic baseline inventory, we cannot determine whether a newly isolated species is an exotic microbe. Such an issue arose in the acid sulfate habitat of *Sulfolobus acidocaldarius* (Brock et al. 1972). This organism was the first species known to grow in this habitat. Then several new species were reported, *Metallosphaera sedula, Sulfolobus metallicus, S. solfataricus, Acidianus brierleyi, A. infernus, Acidobacillus fibrocaldarius, Lobobacillus acidocaldarius* (Zillig et al. 1980, Segerer et al. 1986, Huber et al. 1989, Huber and Stetter 1991, Weiss Bizzoco 1999). It was not known whether they were newcomers to the acid sulfate habitat or were always present, but due to advances in isolation technology, only recently identified and reported

One approach to this question was pursued by Susan Barns and Norman Pace (Barns et al. 1994), who developed a complete inventory of a mineral rich hot spring known as Jim's Black Pool using PCR-based DNA fingerprinting of the small subunit rRNA. This classic study produced a grouping of the archaeal domain into 2 kingdoms, *Crenarchaeota* and *Korarchaeota.* This would not have been possible using traditional enrichment culture techniques, since most of the microbes cannot be cultured.

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[1] This article was originally presented as part of the 5th Biennial Scientific Conference on the Greater Yellowstone Ecosystem held at Yellowstone National Park in October 1999. The conference was entitled "Exotic Organisms in Greater Yellowstone: Native Biodiversity Under Siege." The July 2001 issue of the WESTERN NORTH AMERICAN NATURALIST (Volume 61, No. 3) published presentations and papers from the conference.

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We report herein a baseline inventory of organisms in the acid sulfate habitat based on both historical and recent study. Then we present the opinions of prominent Yellowstone researchers on the possibility of introduction of exotic species of microbes from human (including human researcher) activity.

STUDY SITES

We examined 2 types of acid hot springs in YNP, flowing springs and mixing pools. These thermal habitats are further distinguished by their chemical and physical characteristics. Among flowing springs, the south end of Roaring Mountain is the hottest acid spring (pH 2.1) in YNP, with a site temperature at the origin of 93°C. This compares with the western end of the Amphitheater basin, springs 2 and 3 (pH 2.3), with an origin temperature of 81°C. However, these springs have heavy deposits of sulfur that begin a few centimeters away from the origin. Phenotypically interesting organisms are associated with sulfur deposited along outflow channels (Amphitheater Springs and Norris Junction). No such deposits occur at Roaring Mountain.

In 1971 Norris Junction and Amphitheater Springs were similar in that both sites had flowing springs with sulfur deposits in the outflow channels. Over the years since 1971 at Norris Junction, both temperature and water flow have decreased. The main spring at Norris Junction still has heavy deposits of elemental sulfur. However, the spring is now a mixing pool with a much lower temperature (70°C) than that measured in 1971 (80°C).

We examined several mixing pools in the Norris Geyser Basin: Congress, Vermillion, Locomotive, and Growler (defunct in 1975). We also visited several sites in the Sylvan Springs complex (Gibbon Geyser Basin). Another spring we studied, Frying Pan Spring, lies north of Norris Junction along the road to Mammoth. In the Mud Volcano area we studied Sulfur Caldron and Moose Pool. We examined a series of springs in Hayden Valley located in Crater Hills. These springs are mixing pools; one with a visibly high content of elemental sulfur is known as Great Sulfur Spring.

METHODS

Organisms in flowing springs were examined by immersing cleaned, one end–frosted glass slides in a spring as described previously (Weiss 1973). The slides (RITE-ON, Clay Adams, NY) were cleaned with ethanol (ETOH), rinsed with water, air-dried, and placed in outflow channels of springs. Organisms were allowed to attach and grow for selected periods of time; the slides were then removed, placed in a screw-cap Coplin jar or a small plastic slide carrying case (Cell Path, Hemel Hempstead, UK) filled with spring water, and returned to the laboratory.

For DNA staining, a stock solution of 4′, 6-diamidino-2-phenylindole, HCl (DAPI) stain (10 µg mL^{-1}) was prepared in 0.1 M 2-(N-morpholino) ethanesulfonic acid, MES buffer, pH 6.8, 1 mM ethyleneglycol-bis-(ß-amino-ethyl ether) N,N′-tetraacetic acid, (EGTA), 0.5 mM $MgCl_2 \cdot 6H_2O$. Samples were mixed with an equal volume of stain on a slide to deliver a final concentration of 5 µg mL^{-1} DAPI. In some experiments cells were concentrated before staining by centrifugation at 10,000 *g* for 15 minutes at 23°C.

Samples were observed and photographed with a Leitz Dialux 20 phase contrast epifluorescence (A filter block) microscope equipped with a Wild MPS 55 automatic camera. Images were recorded using Kodak T-MAX 400 film and T-MAX developer.

Electron microscope samples from flowing acid hot springs were taken in the channel center. Samples of sediment were collected with an inverted sterile 10-mL pipette with a tip broken to accommodate a pipet pump. Samples from pools were collected in a 1-L Nalgene beaker attached to a telescoping 8-foot paint roller pole. The samples were transferred into 140-mL plastic bottles.

For electron microscopy, we cooled environmental samples in the field to ambient temperature, ~25°C. Glutaraldehyde (4%) in 4 mM KPO4 buffer, pH 7.0, with 0.1 mM $CaCl_2 \cdot 2H_2O$ and 0.1 mM $MgCl_2 \cdot 7H_20$ was added to an equal sample volume to obtain a final concentration of 2% V/V glutaraldehyde. After fixation for 2 hours at ~25°C, the cells were centrifuged at 8000 *g* for 15 minutes, washed in buffer, and fixed in 1% OsO_4 in 50 mM cacodylate-HCl buffer, pH 7, for 1 hour at 25°C, cooled on ice, and fixed for 4 hours longer. Fixed cells were dehydrated for 10 minutes each in 25, 50, 75, and 100% acetone and embedded in Spurr's epoxy resin. Ultrathin sections cut on a Reichert OMU 2 ultramicrotome with a diamond knife were stained with uranyl acetate and lead citrate.

For negative staining, we placed a small drop of cells on a Formvar plastic-coated grid. Organisms were allowed to attach for 5 minutes. The cells were stained with 2% W/V aqueous uranyl acetate and dried with filter paper. Samples were examined with a Philips 400 transmission electron microscope.

Scanning electron microscope (SEM) samples were prepared on 13-mm-diameter cover glasses. Cells and sulfur attached to cover glasses coated with a thin layer of poly-l-lysine to increase binding of sulfur and cells. Cells were fixed for 1 hour or longer on the cover glass with 1% OsO_4 in 50 mM Na cacodylate, pH 7.2. After dehydration for 5 minutes each in 25, 50, 75, and 100% ETOH, samples were dried by the critical-point method using a semiautomatic Tousimis samdri 790 drier and then sputter-coated with Au-Pd on a Hummer VI. Cells were photographed in a Hitachi model 2700 SEM equipped with a Princeton Gamma Tech IMIX X-ray microanalyzer. Sulfur was identified in the SEM on Au-Pd–coated samples attached to aluminum stubs.

Sampling of YNP Thermobiologists

An abstract was prepared for a conference talk to be presented at the 5th Biennial Scientific Conference on the Greater Yellowstone Ecosystem entitled, "Exotic organisms in greater Yellowstone: native biodiversity under siege." The abstract on potential contamination of YNP thermal springs by human activity was sent (by e-mail) to a selected list of researchers known to be experts in their field and active in YNP microbial research. The e-mail requested comments and opinion on the question for inclusion in the present paper.

Information on sampling methods from one investigator, Karl O. Stetter, was adapted from a video tape (Films for the Humanities and Science 1993) with the approval of the investigator.

RESULTS

Microbial Inventory

HISTORICAL STUDIES.—In the 1970s, *Sulfolobus* was the predominant organism at temperatures above 70°C at Norris Junction and Amphitheater Springs 1 and 2. It could be isolated easily from most sites in both areas either on sulfur as an autotroph or on yeast extract as a heterotroph. It usually took about a week to isolate new strains, sometimes slightly longer, from most sites. At our Roaring Mountain sites, it was the only organism we saw. Here, we define *Sulfolobus* as *Sulfolobus*-like, meaning that the organism was a lobed sphere. It is important to note that at this time we had not yet described it as a genus. We were just beginning to write up the work, which was initially submitted in July 1971 (Brock et al. 1972).

On all of our slide immersion studies, whether at Roaring Mountain, Norris Junction, or Amphitheater Springs, we found roughly equal numbers of attached rods and *Sulfolobus* spheres around 70–75°C. Above 75°C the main organism was *Sulfolobus;* few if any rods were seen. Below 70°C rod-shaped cells began to appear in very high numbers at sites along thermal gradients at Norris and Amphitheater, but not at Roaring Mountain, where we saw principally *Sulfolobus*. Investigators Carl Fliermans and David Smith found metabolic activity in the soils of Roaring Mountain due to both *Sulfolobus* and rods (perhaps *Thiobacillus*). The highest temperature at which they observed rods was about 60°C.

In 1997–98 we surprisingly found mainly rod-shaped cells in the samples from Amphitheater Spring 2. We found many more types than the few we had observed earlier in our 1970–1973 thin-section and negative-stain electron microscopy. In the early samples we saw only 2 different rods at Amphitheater. The first had a *Sulfolobus*-like subunit cell wall, and the second, a long filament, had a layered, bacterial-like cell wall. With so much diversity apparent, it became difficult for us to characterize all the different types of organisms (rod shaped) that were present. When the samples at Amphitheater Springs were prepared and examined by electron microscopy, some *Sulfolobus*-like spheres appeared. But the striking difference was the ratio of rods to spheres at temperatures up to 75°C. Whereas previously there had been about a 1:1 ratio, now the ratio was on the order of 10:1 rods to spheres. We have not yet found a suitable explanation for these dynamics, but the sites have undergone many changes over the years.

We also did slide immersion studies in the same spring in 1997–98 and found no colonies of *Sulfolobus*-like cells at temperatures of 70–80°C but significant attachment of rod-shaped cells. The slides immersed in springs had many elongated, thin filaments (0.4 × 20 μm), rods of medium thickness and length (~0.6 × 6 μm), and smaller rods (~0.5 × 2 μm). Here again, this differed significantly from our earlier observation that *Sulfolobus*-like and rod-shaped cells were present in about equal numbers, but above 75°C *Sulfolobus*-like cells usually outgrew rods on immersed slides and developed into colonies. The slide immersion studies usually correlate well with phase contrast microscopic observations of samples taken from the same habitat.

RECENT STUDIES.—Two other features of these early observations are worth noting. (1) *Sulfolobus*, when it did occur within the deposits of sulfur at Amphitheater Springs 1 and 2, was present in large numbers in microhabitats. (2) It was not seen at every sample site. This compares with rods that were the dominant type in our recent observations. Amphitheater Spring 3 (summer 1997), with unusual dark deposits at the origin and elemental sulfur, had almost totally *Sulfolobus*-like cells and only a few rods. The deposits (perhaps iron) were bound tightly to the siliceous bottom of the spring. Sulfur deposits begin at the origin, and extensive deposits occur further down the thermal gradient.

This difference (rods vs. spheres) is particularly evident when cells are examined by DAPI staining (Fig. 1). Samples taken at 78°C at Amphitheater Spring 2 compared with those from nearby Spring 3, 75–78°C (Fig. 2), emphasize the difference in colonization of sulfur-rich habitats by rods and *Sulfolobus*-like cells. The sulfur crystal structure (c) is particularly evident as are the differences in morphology of the microbes attached to sulfur. The individual rod and spherical shapes can readily be seen by DAPI staining and phase contrast microscopy.

More detail can be observed when cells attached to sulfur are processed for negative staining (Fig. 3). Here, the 2 different cell types and their relative sizes are evident. The *Sulfolobus*-like cell is a lobed sphere ~1 μm in diameter with several thin filaments, termed pili, extending from the cell surface. The thin filaments possibly play a role in attachment of cells to sulfur. The wall structure is formed from subunits arranged in a 2-dimensional array. The rod-shaped cell has a somewhat different cell wall, with small, circular units arranged in rows that form a regular 2-dimensional array. The cell is about 0.45 × 2.6 μm, uniform in width, and has rounded ends. It has no thin filaments or other obvious surface structures. We made an interesting observation on other cells: flagella bearing wings of unknown function. Commonly, 2 of these are arranged opposite each other (180° apart) along the flagellum. They extend from the surface of the flagellum as featherlike rows that run as a helix along the full length of the flagellum (Weiss Bizzoco et al. 2000).

Samples from Amphitheater Spring 2 taken at 70°C, 74°C, and 78°C sites were examined by SEM. The high-temperature (78°C) sample is shown in Figure 4. Here, rod-shaped cells (R) and spherical, *Sulfolobus*-like cells (S) appear in about equal numbers. Both cell types are attached to the surface of crystals. Because there are many different minerals present in hot springs, some of which are crystalline, we examined individual crystals with attached cells. X-ray microanalysis reveals that sulfur (S) is a major component of the crystal to which microbes are attached (Fig. 5). At temperatures of 70°C and 74°C, rod-shaped cells appear by the thousands, while *Sulfolobus*-like cells are seen less frequently in samples examined in the SEM.

Frying Pan Spring is a large pool, pH 2.4, with a temperature of 75°C (vs. 77°C in 1971). In 1971 at Frying Pan Spring, a mixing pool, we saw only rod-shaped microorganisms. One was a long, slender filament just visible by phase contrast microscopy, and the other was a short, sausage-shaped rod. In 1997 when we examined control cells from this spring without the addition of DAPI using fluorescence microscopy, we found no autofluorescence. DAPI staining identifies DNA in several morphological kinds of rod-shaped cells (Fig. 6). The observed DAPI fluorescence coincides with the DNA of cells visualized in phase contrast images of cells. Thin filaments and sausage-shaped cells exhibit DAPI fluorescence with different intensities (Fig. 6). Some cells showed small, intensely fluorescent sites, suggesting they are undergoing cell division.

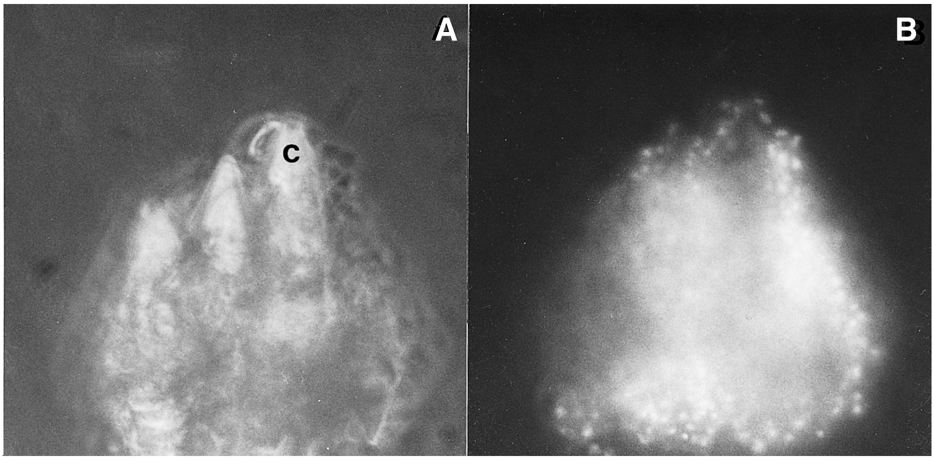


Fig. 1. DAPI-stained *Sulfolobus*-like control sample. Sulfur crystal (c) with attached spherical cells was collected from a flowing spring. A, Phase contrast; B, DAPI stain. DNA is seen as uniform DAPI fluorescence. Amphitheater Spring 3: 75°C, pH 2.3. X1300.

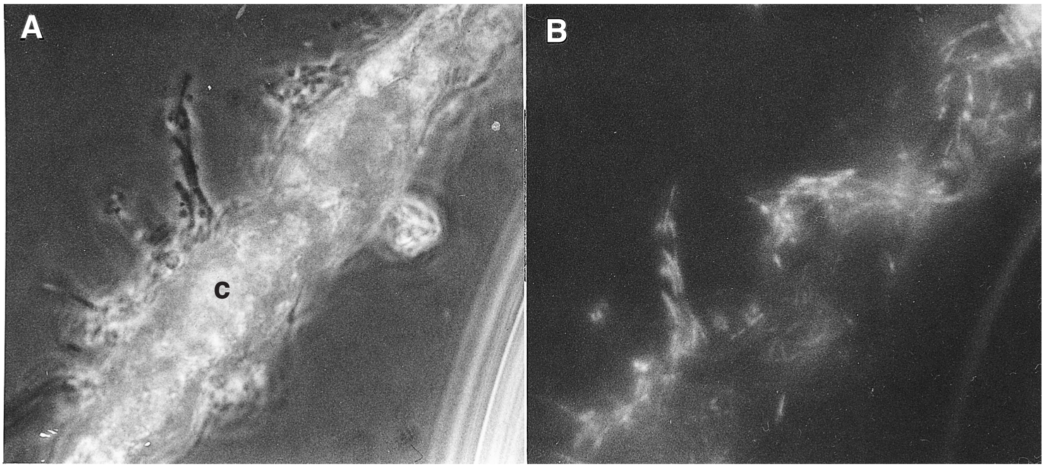


Fig. 2. DAPI-stained, rod-shaped cells associated with sulfur crystals (c) in a flowing spring. Cells attach to crystal (c) and extend from the surface. A, Phase contrast; B, DAPI stain. DNA appears as uniform DAPI fluorescence. Amphitheater Spring 2: 74°C, pH 2.3. X1300.

In contrast, other cells had low levels of fluorescence, suggesting the cells are in the stationary or death phase of the growth cycle. We also fixed cells, prepared thin sections, and examined the resulting cells by electron microscopy. We found thin, microbial filaments and sausage-shaped cells resembling those seen in the light microscope (Fig. 7, cf. Fig. 6). Examination of these by negative staining revealed several different types of flagellated cells (data not shown). Some flagella on these cells lack any obvious substructure, while others are unique in comprising units with a linear substructure. In this sense they are reminiscent of the winged flagella at Amphitheater Spring 2 that also have a linear substructure.

In mixing pools we found 2 distinct populations of cells. In 2 sites there was nearly a pure culture of *Sulfolobus*-like cells. This occurred at Moose Pool and Great Sulfur Spring. Sulfur Caldron, Locomotive, Growler, and several of the springs in the Sylvan

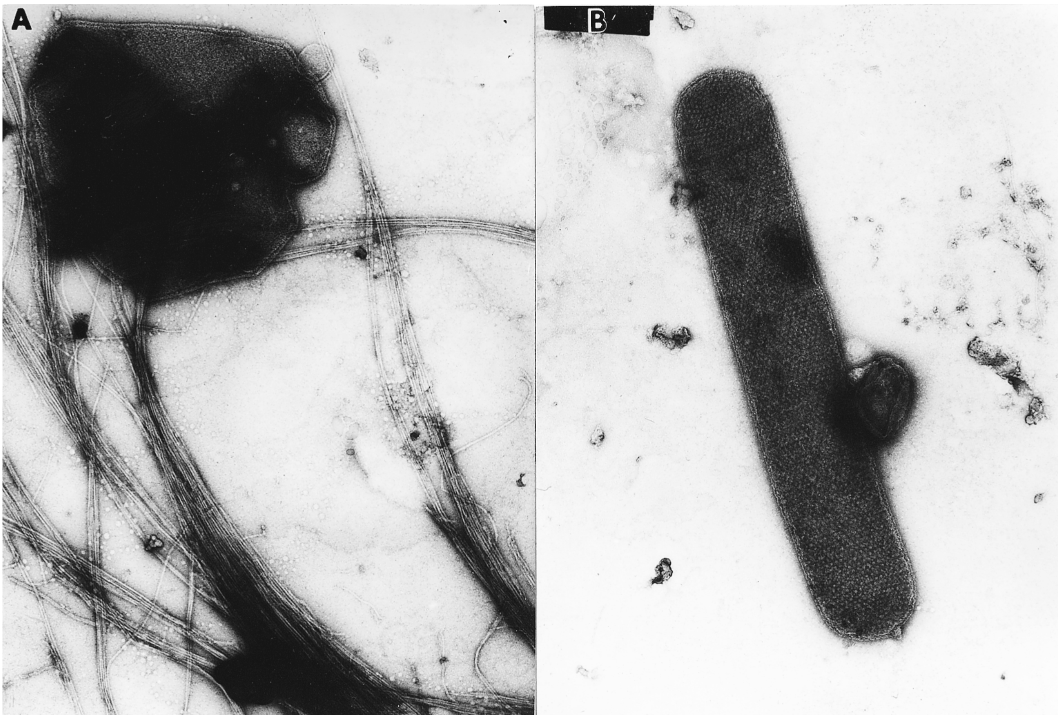


Fig. 3. Microbes attached to sulfur in a flowing spring: A, *Sulfolobus*-like cell is a lobed sphere about 1 µm in diameter. Cell bears thin filaments intertwined with nearby filaments. Cell wall is formed of subunits arranged in a regular pattern over the surface. B, Rod-shaped cell with surface subunits arranged in rows forming a patterned array. Cell shown measures ~0.65 × 2.6 µm. No filaments appear on the cell shown here. A, B, Amphitheater Spring 2: 74°C, pH 2.3. Negative stain electron micrographs, X30,000.

Springs area had a mixture of rods and *Sulfolobus*-like cells. In contrast, only rod-shaped cells were observed at Frying Pan Spring, although it is known to contain *Thermoplasma* (Segerer et al. 1988), a spherical organism. From 1971 to 1999 there was a significant change in 2 springs, Evening Primrose and Growler. In 1995 Evening Primrose (Sylvan Springs, see Fig. 6.7b, Brock 1978) caved in. When we visited it in 1997, the temperature had dropped from 89°C (1971) to 33°C. Whereas previously it had been a *Sulfolobus* habitat, it now contained mainly algae and no *Sulfolobus*-like cells. The second spring, Growler, had collapsed earlier (1975), and above (northeast) it a new spring, Sulfur Spring, appeared. From 1997 to 1998 Sulfur Spring changed in temperature from 88°C to 74°C. Despite such changes, the microbial populations of most mixing pools remained relatively stable over the period from 1971 to 1999. Our most recent microbial survey of these springs is presented in Table 1.

Human-vectored Contamination: Perspectives of Yellowstone Microbiologists

Thomas D. Brock

E.B. Fred Professor Emeritus, Department of Bacteriology, University of Wisconsin, Madison. Area of study: Thermophiles

Although human cross-contamination could occur, it seems to me that this process would occur much more often via wild animals in the area, or via airborne contamination. Sorting out human from nonhuman contamination experimentally would be difficult.

Craig J. Oberg,

Department of Microbiology, Weber State University, Ogden, UT. Area of study: Metabolism and genetics of thermophiles

Lower temperature acidic and photosynthetic environments are continually inoculated by environmental biota and are thereby probably immune to xenic species contamination. Hyperthermophilic habitats, although refractory to most species, are

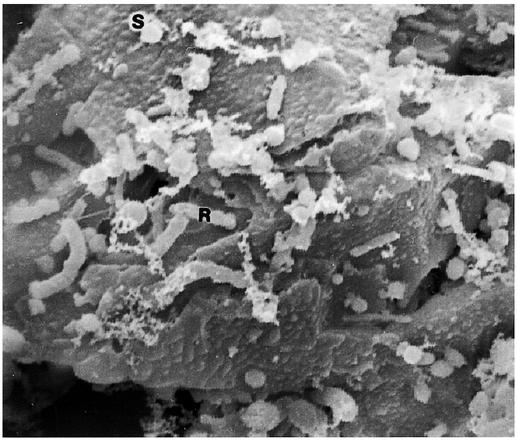


Fig. 4. Rod-shaped (R) and *Sulfolobus*-like (S) cells attached to sulfur in a flowing spring. Amphitheater Spring 2: 78°C, pH 2.3. Scanning electron micrograph, X2300.

not often visited by natural vectors and may be inoculated only by contaminated human probes.

Richard W. Castenholz

Department of Biology, University of Oregon, Eugene. Area of study: Yellowstone photosynthetic thermophiles

With present practices I do not believe there is a real danger of introducing exotic microorganisms into Yellowstone hot springs. First of all, most thermophilic microorganisms from far distant hot spring clusters (which are by their nature disjunct) would be rarely transported in sufficient inoculum size to become established in a hot spring community (usually of different chemistry). It is a "principle" of ecology that established native communities rarely become displaced by exotics unless the recipient community is disturbed. This may also apply to hot springs communities. Sufficient inoculum may come frequently enough from hot springs in the same cluster (e.g., the springs of Yellowstone), by insects for example, but this would be expected and constitute natural dispersal. Although thermobiologists are probably the most likely vectors of viable cells from one geothermal area to another (e.g., Oregon to Yellowstone), the amount of inoculum would be essentially inconsequential, i.e., some old mud on boots, unwashed collecting equipment, etc., unless of course there is a purposeful mass inoculation. Nevertheless, I have always made it a practice to use new materials or sterilized old. Scrubbing boots and/or steam sterilizing them or simply using a new pair is a good idea if collectors have been in a distant hot spring area. I am sure that transferring boats from one lake or temperate stream to another constitutes a much greater risk (well documented) of introducing exotic species than in the refractory habitat of hot springs. The natural photosynthetic populations of alkaline and acid hot springs and their patterns in Yellowstone have not changed in any apparent way during the past 33 years of my studies, but of course this does not include the more recent studies using molecular methods. As for the shift in dominant species in various springs, there are well-documented changes in the chemistry, temperature, and flow in many springs in Yellowstone, especially in unstable areas such as Mammoth and Norris. I have observed many pH and temperature changes in springs over these years, and these changes correlated with some changes in microorganisms. As for the "possible" shift from *Sulfolobus* to *Acidianus* in some acid springs, the latter genus was unknown earlier and would not have been recognized at that time in the 1970s when *Sulfolobus* was discovered. Even if such a shift has taken place, in order to understand it, studies of correlative changes in temperature, pH, and chemistry should have been made in order to find possible causes. The introduction of *Acidianus* by collectors or human vectors of any type seems (by orders of magnitude) the least likely scenario.

As far as other impacts of hot spring collectors are concerned, taking an occasional thimbleful or even 100 mL of water and mat/sediment is not going to affect in any way the integrity of the hot spring community of microorganisms. However, trampling of soil and plants surrounding certain heavily used hot springs (e.g., Octopus Spring) should be discouraged as much as possible. There are many springs similar to Octopus that could be used by collectors.

Norman R. Pace

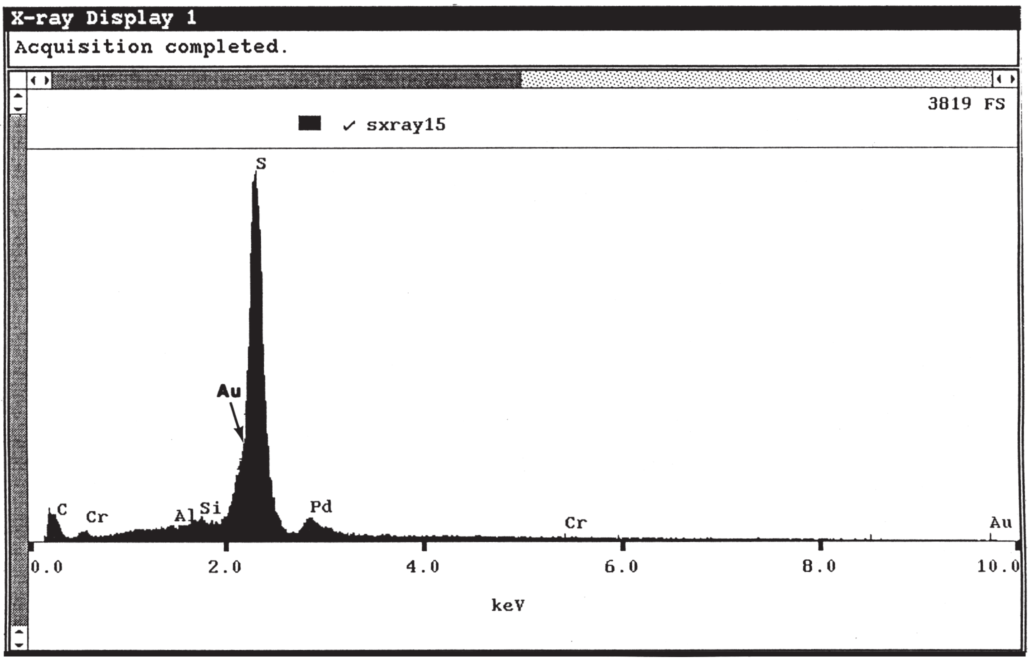
Department of Molecular, Cellular, and Developmental Biology, University of Colorado, Boulder. Area of study: Biodiversity—PCR-based DNA fingerprinting

I'm in full concurrence with Brock and Castenholz about this. I'm not too concerned about contamination (of Octopus Spring or Obsidian Pool) because the mats are so rich in biomass. We always try to use aseptic technique and are less concerned about contaminating the site than the sample.

Carl R. Woese

Department of Microbiology, University of Illinois, Urbana. Area of study: Gene isolation techniques

Although the direct gene isolation method now fails us by not identifying the actual phenotype of the organism from which the gene has come, the approach more than compensates for this by (1) telling us that phenotypically characterized organisms are related to unisolated ones; (2) allowing us to



X-ray Display 1

Acquisition completed.

Fig. 5. X-ray spectrum of crystal sampled at Amphitheater Spring 2: 78°C, pH 2.3. Sulfur (S) is a major component. The gold-palladium (Au-Pd) peaks represent the surface coating deposited on the crystal during sample preparation. Also evident are aluminum (Al) from the sample stub and carbon (C) from cells. Chromium (Cr) and silicon (Si) are present in the sample as minor components.

design probes and primers to aid in efforts to isolate the organism in question by enrichment culturing; (3) best of all, having the potential of a complete accounting of microbial species occurring in a niche, complementing enrichment culturing. Together, the 2 approaches give microbiologists the power to define, understand, and reveal the full richness of the microbial world.

Francisco F. Roberto

Department of Biotechnology, Idaho National Engineering and Environmental Laboratory, U.S. Department of Energy, Idaho Falls, ID. Area of study: PCR-based Yellowstone microbial extremophile diversity

On *Acidianus brierleyi,* I don't believe it's an alien species, but actually it has probably been there all the time. It's likely that it was in Brock's original enrichments, as it's virtually indistinguishable from *Sulfolobus acidocaldarius* under a microscope. I'm not surprised by Brock being cool to the idea. I saw the call for papers and also think that rather than introducing new microbial species, the biggest effect of man is altering the environment, leading to the succession and dominance of "non-native" species, which have probably always been around in small numbers, but not had the right environments to proliferate.

Karl O. Stetter

Department of Microbiology, University of Regensburg, Regensburg, Germany. Area of study: Hyperthermophilic microbes

I define hyperthermophilic microbes as those growing fastest above 80°C. I isolate hyperthermophiles from many terrestrial, subterranean, and abyssal and shallow submarine areas all over the world. From Yellowstone (I have had a collecting permit for about 15 years), my co-workers and I have cultivated and described (1) *Thermoplasma volcanium,* the first *Thermoplasma* (wall-less microbe) in YNP; (2) *Thermosphaera aggregans,* from Obsidian Pool; (3) *Thermocrinis ruber,* Brock's "pink filaments," from Octopus Spring. For sampling and storage of samples, I always use glass bottles to avoid diffusion of oxygen into samples. This would occur with plastic bottles.

Like other Yellowstone investigators, Karl Stetter samples hot springs in a temperature range from 70°C to boiling water. In addition to Yellowstone, Solfatara Crater near Pozzuoli, Italy, is one of his choice hot habitats; it is laden with sulfur. Sampling here at extreme temperatures, he is most concerned with keeping the organisms happy. To sample an inaccessible spring, he uses a long, 2-piece pole with a small 250-mL stainless cup attached to one end. He fills up the cup by sampling in the

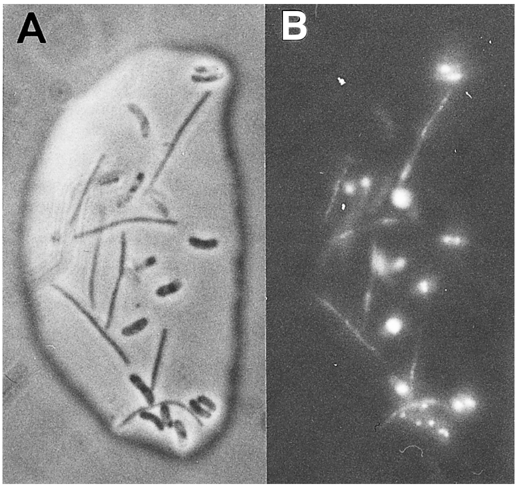


Fig. 6. DAPI-stained cells from a mixing pool. A, Phase contrast; B, DAPI fluorescence. DNA appears as bright spots or less intense thin lines of DAPI fluorescence. Frying Pan Spring: 75°C, pH 2. X1300.

middle of a spring and transfers the sample to a glass sample bottle that he fills to the top without introducing bubbles during pouring. In springs that are easy to sample, he uses a 50-mL plastic syringe to withdraw samples. Here again, he fills up a glass bottle to the top to exclude oxygen. Then he may add sodium dithionite to the sample. He notes, "There is one important thing, there is practically no oxygen here. With a powerful oxygen killer, sodium dithionite, the organisms will be very happy" (Films for the Humanities and Science 1993).

Robert F. Ramaley

Department of Biochemistry and Molecular Biology, University of Nebraska Medical Center, Omaha. Area of study: *Thermus* species

As of this point, I don't know if we have any hard data that "native microbial populations" in Yellowstone have been displaced by either "native" transfer (wildlife) or any evidence that investigators themselves could be contributing to displacement from any use of nonsterile collecting equipment. This is a constant worry, especially when you see investigators doing physical sampling of hot springs for released gases, etc., much as I observed on 16 July 1999 at Octopus Spring by Gavin Chan and other students from Washington University in St. Louis during their detailed mapping of the outflow channels of Octopus Spring (Web site http://epsc.wustl.edu). I have been very careful to always use sterile materials (wrapped sterile sampling material) and suggest that approach for other individuals or investigators to avoid or minimize any direct contamination problems.

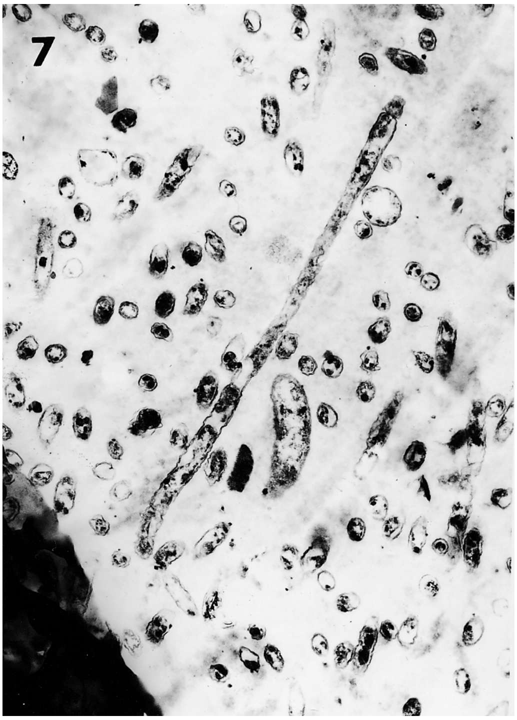


Fig. 7. Thin filaments and wide, curved rod coexist with other cell types in a mixing pool. Figures 6 and 7 may be compared. Frying Pan Spring: 75°C, pH 2. Thin-section electron micrograph, X10,000.

Perry Walker Russell

Department of Biology, Cumberland College, Williamsburg, KY. Area of study: Sampling protocol

A sampling protocol needs to be established that will preserve these sites as much as possible. Since my background is in pathogenic bacteriology, I have always as a habit used techniques that are as close to "sterile technique" as possible. (1) I use a telescoping golf ball retriever with a glass beaker attached to the end for gathering my samples and a thermometer hanging from the end of the retriever shaft. (2) Before collecting a sample, I sterilize the end of the retriever, the beaker, and the thermometer with alcohol. (3) When actually collecting the sample, I never stand in the water and, in fact, like to stand back a little way. Of course, for really hot or dangerously weak crustal areas, standing back is a necessity, but I also like to stay back a couple of feet from more easily accessible and cooler runoff streams. After all, I don't need to be stomping around with my Kentucky microflora–laden boots in Yellowstone thermal springs. (4) Upon retrieving a sample in the beaker, I first check the temperature reading and then pour the sample into an individually wrapped sterile polypropylene tube

TABLE 1. Microorganisms in acid thermal habitats in Yellowstone National Park.

Location	°C	pH	Microbes[a]
Amphitheater Spring 2	78	2.0	*Sulfolobus*-like, thin filaments, short wide rods, flagellated rods
	74	2.0	*Sulfolobus*-like, long curved rods, thin rods, one enlarged end, short rods, winged flagella
	70	2.0	short wide rods
Norris Geyser Basin			
Sulfur Spring above Growler	88	1.5	long rods, short rods, thin rods
Locomotive	83.5	2.0	*Sulfolobus*-like, short rods
Vermillion	79	2.3	*Sulfolobus*-like, short rods, thin rods
Congress	85.5	2.6	short rods
Small Triangular Pool	86	2.1	Sulfolobus-like, thin rods, wide rods, curved rods
Norris Junction	72	1.5	*Sulfolobus*-like, thin rods, wide rods, long, irregular curved rods, long rods
Frying Pan Spring	75	2.4	Thin filaments, medium length rods, long rods, short curved wide rods
Roaring Mountain			
(southern effluent)	88	2.2	*Sulfolobus*-like, long thin filaments
	80	2.2	*Sulfolobus*-like, short rods
Mud Volcano area			
Sulfur Caldron	70	1.5	*Sulfolobus*-like, *Lobobacillus,* long thin rods, short thick curved rods, short thin rods
Moose Pool	69	1.8	*Sulfolobus*-like, thin filaments, very thin rods, wide rods
Crater Hills			
Great Sulfur Spring	86	2.1	*Sulfolobus*-like, a few short thin rods

[a]Sampling period was 1997–1999.

(maybe 8–10 mL). The residual in the beaker I pour out into the dirt or sand (not back into the water). (5) I can now take a pH reading of my sample by quickly putting a drop or two from my sample tube onto pH paper. (I tend to prefer this method over sticking a probe end into the spring or the sample because of the potential for contamination plus I have always found my pH test strips to be accurate enough for my purposes.) (6) Before moving to the next site, I record my site data (temperature, pH, location, and elevation) and sterilize the end of the retriever, the beaker, and the thermometer with alcohol again.

Hopefully by using this protocol, I am not contaminating any sampling site with bugs from Kentucky or cross-contaminating springs with other thermophiles. My only worry lies in the fact that while alcohol should destroy any bacterial contaminants, it may not eliminate all bacteriophage contaminants.

DISCUSSION

Several kinds of experimental approaches provide a microbial inventory of hot spring ecosystems. These include (1) PCR-based methods to amplify rRNA gene sequences (ribosomal DNAs), (2) DNA staining with DAPI to distinguish microbes from minerals, and (3) electron microscopic analysis to identify microbes and their phenotype. Small subunit rRNA sequence-based analysis provides the most complete inventory of microbial populations. While this method does not assess the microbial growth phase or phenotype of unknown microbes, as do DAPI staining and electron microscopy, it provides an elegant method to gain information on microbes that can be seen microscopically, but not cultured. Such approaches are strengthened by microbial culture and an analysis of phenotypes to reveal the presence of new characteristics such as the “winged” flagellum (Weiss Bizzoco et al. 2000).

Our observations of *Sulfolobus*-like cells in pools ranging in temperature from 68°C to 88°C and in a flowing spring at Amphitheater (79°C) indicate that in many acid habitats this is the dominant morphological type of organism. It is also clear from our results that population dynamics in mixing pools have not changed substantially since 1971 when cells of environmental samples were first observed by means of electron microscopy. It seems clear from our results of the past 3 years that a morphologically diverse collection of rod-shaped microbes exists at 70–89°C, pH 2–2.4. This temperature range is substantially higher than that reported for most rod-shaped thermophiles in comparable habitats below pH 3. The exceptions perhaps are *Thermofilum* and *Thermoproteus,* which grow anaerobically (70–97°C, pH 2.5–6.5) and share *Sulfolobus* habitats (Stetter 1986).

Our studies show that in one flowing spring at Amphitheater a substantial change has taken place. Whereas our earlier study (Weiss 1973) showed that at temperatures above 75°C *Sulfolobus*-like cells were the predominant cell type, we have demonstrated here that rod-shaped microbes significantly outnumber *Sulfolobus*-like cells at all temperatures above 65°C in Amphitheater Spring 2. Our light and electron micrographs indicate that in this spring there may be significant interactions among phenotypically diverse rod-shaped cells as well as between the rod-shaped cells and spherical *Sulfolobus*-like cells. Such cell-cell interactions may allow survival of the associated cell types and appear to involve direct attachment by cell walls or short surface pili. One feature of considerable interest is that whether cells attach to sulfur directly, as with rod-shaped organisms, or by pili, as with *Sulfolobus*-like cells, the majority of the attached cluster remains separated from the sulfur crystal surface. *Sulfolobus*-like cells accomplish this by means of long pili, whereas rods attach to each other, forming elongated cell groups that extend away from the sulfur crystal. The significance of this separation distance for the oxidation of sulfur and the long-term survival of the microbial community remains to be determined.

The finding that *Sulfolobus*-like cells no longer represent the dominant organism at Amphitheater Spring 2 indicates that a change in population dynamics has occurred. We note with interest that it is still the most abundant microbe in nearby spring 3 in the Amphitheater group. At another flowing spring, Roaring Mountain, changes are not as obvious because of lower cell numbers and the absence of sulfur. This type of microbial community change has been considered by Yellowstone microbiologists who generally believe that other organisms have always been present along with *Sulfolobus,* and that a shift in the dominant species does not result from research activities but instead represents natural succession within native microbial communities. In keeping with that opinion, it seems unlikely that the change represents an "invasion" or exotic microbes. It is also unlikely that this habitat has been intentionally disturbed by research or other human activity. The pH and temperature of this site have been rather stable over the years. However, changes such as flow rate, chemistry of the spring, or nutrients entering from the algal mat above the spring may all be factors contributing to microbial changes.

Human-vectored Contamination

This study shows that microbial community changes have occurred over a period of time in the acid hot spring habitat. An important question is whether such changes might be expected to occur naturally over time within an established community or whether they might be the result of human research activities. We will consider below 5 points related to this question, i.e., human-vectored contamination.

(1) *The argument is given that human and animal contamination would be hard to separate.*

While this is most likely correct, animal cross-contamination might be more easily dismissed. Although animals such as moose and bison range in the area of acidic hot springs and pools and might step into a spring, transfer of acquired microbes seems more likely limited to nearby springs which themselves have already been exposed, possibly through abiotic processes, to these same organisms. With springs that are more distant, say miles apart, it could take many hours for the animal to travel to the next spring, and the microbes might die or be removed during transit time from the first to the second spring.

The time interval for springs several miles apart would be so great that such cross-contamination is less likely. Insect-mediated contamination may have a shorter interval for the longer distances, but insects for the most part would likely be limited to the cooler surfaces of algal mats below 55°C. Furthermore, microbial communities in these mats have long been exposed to insect foraging activities, particularly ephydrid flies that carry out their life cycle year-round in algal mats. Possible dispersal of microbes in these lower temperature ranges seems to be part of the biotic activities to which springs and microbial communities have already been exposed. At the lower temperature ranges, there is a complex community structure. Algae constitute a food source for these herbivores (Brock 1978), but at higher temperatures insects do not seem to visit the springs to any great extent.

On the other hand, investigators travel by automobile from one site many miles to the next, within minutes. The general mobility of investigators who can travel rapidly from site to site and the presence of inexperienced investigators such as graduate students or assistants represent unknowns that could impact hot spring habitats. While researchers are well aware of and concerned about exotic species, the current awareness was not a major concern with microbes one or more decades ago.

We should note that even if mud from an investigator's boot were to enter a new system accidentally, most of it would be carried downstream in a flowing spring like Amphitheater, leaving only a small and likely inconsequential amount of inoculum. In pools this could vary a bit where there might not be an outflow channel. Most pools are sampled with some type of extension device so that investigators stay further away from the edge of a pool than they would a flowing spring. Despite the lack of past attention to possible contamination, microbial investigators have always been careful to try to minimize input in hot springs and pools and in most cases use sampling methods and devices that would avoid any but the smallest possible input into a system. The fairly sizeable flow rate of spring water in pools and the continuous turnover of the contained water (Brock 1978) would likely remove the introduced inoculum.

(2) *Microbial researchers are very careful to avoid contamination of their samples, but in the past they may not have been thinking about mud or soil that was on their feet.*

Moreover, investigators taking hot spring samples to analyze physical or chemical properties may not have been as careful as microbiologists. So, both seem to be likely potential vectors.

Although this concern introduces an unknown, it is diminished somewhat because acid hot springs provide a hostile environment, perhaps even for the resident microbes. This is seen by our DAPI staining results where most cells in the springs are in a stationary phase and are not growing and rapidly dividing. Very few organisms present have been isolated in culture. This is usually consistent with stringent nutrient (or oxygen) requirements. As pointed out by Stetter (Films for the Humanities and Science 1993), many acid hot spring organisms utilize hydrogen and are inhibited or killed by oxygen. This implies that exotic organisms have complex growth requirements that likely will not be met in most new habitats.

(3) *Castenholz argues that exotic species tend to establish only in disturbed habitats, and since these hot spring habitats are thought to be undisturbed, it is unlikely that any of the established species are introduced.*

This is said despite the fact that some changes in communities have been observed over the years. While it seems clear that disturbance facilitates establishment of exotics, this system of hot springs is much more like a series of islands than vast tracts of continental land. In islands dispersal is a rare event, and unique and interesting species arise through adaptive radiation due to the large number of unfilled niches. Islands are prone to exotic species damage even when very undisturbed. When exotic species, e.g., rats, enter a Pacific island, they rapidly establish and decimate the local species, both competitors and local flora. It is easy to imagine that acid hot springs can have very unusual and unique species, but that an introduced bacterium from another pond will not have the bacteriophage load and may actually be better adapted. There might be underadapted species that are susceptible to competitive exclusion by introduced species. Islands can possess underadapted species because of the absence of introduced competitors and predators.

If bacteriophage in cells of the native community were lysogenic, their presence probably would not alter the ability of native cells to compete effectively with an introduced species. On the other hand, if bacteriophage are thought of as a means for keeping microbial populations in check, then a phage-free introduced organism could gain an advantage. If bacteriophage kill off the dominant species (by lysis), this might allow the introduced microbe to gain a competitive advantage and become established in the new ecosystem, assuming all other things are equal.

Although the existence of bacteriophage introduces some uncertainty, it is less of a concern than it might seem. So far, only 2 genera have been recognized as having bacteriophage or viruslike particles (Stetter and Zillig 1985). While this might seem to be a low number of organisms with bacteriophage, recall that we have examined a very large number of springs by electron microscopy of thin sections and whole mounts and find this to be consistent with our results. As for the 2 genera we know about, each has elements that decrease the possible problem. The bacteriophage of *Thermoproteus* cause cell lysis when the sulfur supply is exhausted; clearly, this might be cause for concern, but this organism is a strict anaerobe. This considerably reduces the concern because anaerobic contaminants are not likely to survive transfer via a human vector. Viruslike particles in *Sulfolobus* do not appear to affect active growth of this organism. The crystalline particle arrays seen in *Sulfolobus* are not known to cause cell lysis without an induction mechanism such as UV irradiation (Stetter and Zillig 1985); this required stimulus would not likely be encountered in the natural habitat.

Certainly a case can be made that underadapted species exist within acid hot springs because there is electron microscopic evidence for the existence of a rich diversity, and yet many cells are present in low number. It is easy to imagine that an exotic species might be better adapted than the underadapted species. This introduces some uncertainty, but the niche of the underadapted species would likely be small since they are few in number. So, the introduced species, even if successful, would likely be insignificant.

(4) *One researcher stated that alcohol cleaning would not eliminate bacteriophage contaminants.*

Introduced bacteriophage could be a major disturbance in these systems. Bacteriophage are strongly resistant, perhaps even to attempts at sterilization by ETOH. Bacteriophage in the acid sulfate habitat likely follow the general rule that those with a wide range of species are more rare than those with species or strain specificity. Phage would have to make specific contact with sensitive cells. This might be difficult in a flowing spring with continuously moving water. In a mixing pool bacteriophage could be removed by nonspecific adsorption to a surface such as a mineral particle. Even direct contact with a suitable host would not assure a productive infection. We mentioned that most organisms in these habitats are not actively growing and dividing. Thus, while these considerations (a narrow host range and a quiescent microbial host population) certainly do not eliminate the potential for bacteriophage to disturb the system, the problem is diminished to some extent from a conceptual point of view because the more abundant the bacteriophage might be, the less likely they are to interact effectively with the existing microbial population. In keeping with this idea, viruslike structures in thermoacidophilic cells from natural samples or cultures were seen only rarely (Weiss Bizzoco 1999) in many hundreds of samples examined by electron microscopy. Thus, even if bacteriophage present in these springs are vectored by humans, their activity is likely to be at a low level.

(5) *Although we have stated that these systems do not vary, several springs show minor temperature changes or major changes induced by cave-ins.*

Castenholz mentions documented natural changes in many springs in YNP, especially in unstable areas such as Mammoth and Norris. These natural changes could be the source of disturbance that would enhance the chance for success of introduced exotic microbes.

While solfatara basins such as Norris or Amphitheater Springs seem fundamentally unchanged and stable, individual springs can and do undergo alterations. Far from being unusual, changes of this type, both minor and major, are normal events in solfatara areas. Such natural changes as water flow, temperature, pH, and chemistry all conceivably could enhance or reduce chances for success of human-introduced species. Several arguments should be considered in evaluating which possibility is more likely. First, with present microbiological methods, numbers of any introduced organisms would be small. The likelihood of their becoming established seems low because they would have to undergo an abrupt, and not necessarily favorable, change in chemistry compared to their native habitat. One possible result is that introduced organisms would be washed away or die from these changes. Second, organisms may be introduced to a habitat, but, if not optimally adapted, their numbers will remain low or insignificant. The chances that a few introduced microbes will land in an acid hot spring may be great, but the likelihood of landing in a spring, whether disturbed or not, to which they are optimally adapted in temperature, pH, and flow or chemistry seems minimal. Third, the physiological state of these organisms is an important consideration that is usually overlooked. Most cells in springs are in the stationary growth phase and potentially quiescent. As a result, they are not necessarily going to grow, even if exposed to an appropriate and favorable environment. Fourth, organisms in acid hot springs are exposed to extremes of temperature, pH, and redox potential. Low redox potentials (anaerobic habitats) exist in these springs. Because of the low solubility of oxygen at high temperature and the presence of reducing gases like hydrogen sulfide, most of the organisms are anaerobes. Oxygen is toxic to these exotic organisms, particularly during transfer between springs. This toxicity would likely reduce their ability to displace native microbes or even survive. Fifth, many respondents in this paper are long-time thermobiologists, some with decades of experience. Over the years of attempting to grow organisms seen microscopically in samples, experienced investigators know it may be extremely difficult to duplicate conditions required for growth. This suggests that the organisms have complex nutritional requirements or interactions in their natural habitats. The fastidious nature of these microbes is not particularly evident in native communities where these organisms coexist in large numbers. Introduced organisms with unique nutritional requirements might survive in a new habitat for a prolonged period of time, but it is much less likely that they would displace native residents, even in the face of natural changes or disturbances in a spring.

Taken together, these 5 points on human-vectored contamination introduce some unknowns that may be cause for concern. Although some human-vectored species might survive, if introduced into springs, our rebuttal arguments favor the view that exotic species are likely to have a low probability of displacing native microbial communities, even with the present level of research activities in the acid hot springs of YNP. Because unknowns exist, the use of sound microbiological technique in sampling acid thermal habitats seems absolutely essential to provide the most protection for the unique native microbes.

CONCLUSIONS

Results of this study suggest that the microbial flora in YNP has changed in some cases, and some things not seen in the 1970s may now be present in the system. Whether this is a result of biotic or abiotic processes, including successional change, or introduction of new exotic species (human-vectored contamination) cannot be determined from the results presented here. While the consensus of prominent YNP microbiologists is that research activities have not produced human-vectored contamination, the question has not been studied in detail (using PCR-based analysis), and uncertainty on the issue remains. It will serve the long-term stability of YNP hot springs as well as other similar resources if all investigators (both beginning and experienced) are aware of the possible introduction of exotic species into the springs and thermal sites that are being studied. With care and consideration on the part of investigators, undisturbed hot spring microbial populations will have the best chance to exist for the benefit of future generations. Significant contributions already made include the discovery of life at high temperatures, the invention of PCR (Saiki et al. 1988), and establishing the Archaea as one of the primary lines of evolutionary descent (Woese et al. 1990). That YNP has fostered these contributions suggests that microbial research represents an important activity.

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GEOGRAPHY OF EXOTIC PLANTS ADJACENT TO CAMPGROUNDS, YELLOWSTONE NATIONAL PARK, USA

Karen Allen[1] and Katherine Hansen[2]

ABSTRACT.—Eleven campgrounds in Yellowstone National Park were studied to determine the geography of 10 specific exotic plant species adjacent to campgrounds. Exotics were found in only 6 campgrounds. Six species were found at Mammoth campground, a low-elevation, dry site with year-round use. Only 2 species were found in the other 5 campgrounds. Exotics decreased with distance from Mammoth campground out to 6 m and then increased, suggesting a spread in their distribution. Significant associations were found between exotic presence and both open and closed canopies and low levels of disturbance. Generally, exotics decreased with an increase in cover of other vegetation forms. Five species were found most frequently in big sagebrush habitat types.

Key words: exotic plants, campgrounds, disturbance, canopy cover, Yellowstone National Park.

Exotic plants have dramatically transformed vegetation of the western United States over the past century and can be found today in most disturbed wildlands. Their well-documented ability to displace native species is a primary concern regarding their presence in national parks (Marion et al. 1985, Mack 1986, Weaver and Woods 1986, Bedunah 1992, Cheater 1992, Kummerow 1992, Tyser and Worley 1992, Lesica and Ahlenslager 1993). The introduction and spread of exotic plants into national parks threatens the structure and functions of native plant communities. Previous studies have found exotics to be associated with road and trail disturbance, high light intensities provided by open canopies, and trampling in campsites (Dale and Weaver 1974, Cole 1981, Forcella and Harvey 1983, Kuss and Graefe 1985, Baker 1986, Cole and Knight 1990, Benninger-Truax et al. 1992, Tyser and Worley 1992).

In 1994, 140 exotic species were found in Yellowstone National Park, while in 1986 only 85 were known to occur there (Yellowstone National Park 1986; J. Whipple, Yellowstone National Park botanist, personal communication 1996). It was hypothesized that some of this increase might be related to activities within campgrounds. More exotics were expected to be found close to campgrounds where a source of seeds may have been introduced by humans, cars, and maintenance equipment; where ground disturbance had created areas that could serve as seedling establishment sites; and where the overstory canopy may have been opened for campsites. With that in mind, the objectives of this study were to determine whether exotics were distributed according to (1) distance from campgrounds, (2) amount of canopy (overstory) cover, (3) amount of disturbance, and (4) amount of ground cover.

STUDY AREA AND METHODS

We studied all 11 vehicle-accessible campgrounds of Yellowstone National Park, USA. The campgrounds (1820–2425 m elevation) occur within habitats ranging from big sagebrush/bluebunch wheatgrass (*Artemisia tridentata/Agropyron spicatum*) at lower elevations to subalpine fir/grouse whortleberry (*Abies lasiocarpa/Vaccinium scoparium*) at higher elevations (Table 1). Average annual precipitation near the 11 campgrounds ranges from 37 to 105 cm, and frost-free days range from 21 to 125 (Natural Resources Conservation Service 1994). Campgrounds range in age from approximately 30 to 78 yr. Overnight use today consists primarily of campers with automobiles and, secondarily, of hikers and bicyclists. While the type of use within campgrounds is relatively homogeneous, the number of campers varies substantially and is

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Table 1. Habitat types and related elevations and mean canopy covers in which exotic plants were found in Yellowstone National Park campgrounds.

Habitat type	Elevation range (m)	Campground(s)	Number of transects	Number of transects with exotics	Transect frequency (%)[a]	Exotic species found[b]	Mean canopy (%)[c]
Big sagebrush/blue bunch wheatgrass	1820	Mammoth	8	8	100	SK, YSC, HT, MULL, CT, DT	14
Big sagebrush/Idaho fescue	1895–2090	Slough Creek Pebble Creek	8	2	25	CT	0
Douglas-fir/common snowberry	1895–2000	Slough Creek Tower Fall	6	1	17	CT	0
Engelmann spruce/sweetscented bedstraw or horsetail	1895–2090	Slough Creek Pebble Creek	7	1	14	CT	27
Subalpine fir/twinflower	2000	Tower Fall	3	0	0	none	n/a
Subalpine fir/pinegrass	2060–2275	Norris	21	2	14	OD, CT	6
		Indian Creek					
		Madison		1		CT	
Subalpine fir/grouse whortleberry	2075–2425	Canyon	35		9		21
		Grant Village		1		CT	
		Norris					
		Bridge Bay		2		CT	
		Lewis Lake					

[a] Transect frequency: percentage of transects in a given habitat type that contain exotics.

[b] Key to exotic species found: SK = spotted knapweed, HT = hound's-tongue, CT = Canada thistle, OD = oxeye-daisy, DT = dalmatian toadflax, YSC = yellow sweetclover, MULL = common mullein.

[c] Mean canopy refers to quadrats in which exotics were found.

dependent on the number of sites within a campground and the length of time a campground is open (Wert 1994). Mammoth campground, located near the park's headquarters, is the only one open all year.

Ten exotic species were selected for study based on their designation by park staff as high priority for control (Yellowstone National Park 1986). These included spotted knapweed (*Centaurea maculosa*), hound's-tongue (*Cynoglossum officinale*), Canada thistle (*Cirsium arvense*), oxeye-daisy (*Chrysanthemum leucanthemum*), dalmatian toadflax (*Linaria dalmatica*), yellow sweetclover (*Melilotus officinalis*), Russian knapweed (*Centaurea repens*), musk thistle (*Carduus nutans*), tansy aster (*Tanacetum vulgare*), and common mullein (*Verbascum thapsis*). Species nomenclature and verification of alien status follow Hitchcock and Cronquist (1973). All species, except yellow sweetclover, are also considered noxious weeds by the states of Wyoming, Montana, or both. A noxious weed as defined by federal law is a plant of foreign origin that can directly or indirectly injure agriculture, navigation, fish and wildlife, or public health (Yellowstone National Park 1986, Bedunah 1992).

We systematically established 8 transects, with a random starting point, outward from and perpendicular to the edge of each campground. The edge was located where ≤10% vegetative cover existed adjacent to the campground road's outer border. To identify the distance at which exotic occurrence changed, we sampled contiguous quadrats (4 × 1 m) along each transect from just inside the campground edge (quadrat 0) to 15 m outside the edge (quadrat 15). Additionally, quadrats were sampled at 20, 25, 30, 40, and 50 m from the campground edge to determine the extent of occurrence at greater distances. Eight quadrats inside each campground and 8 control quadrats outside each campground were also sampled for comparisons. Data collected within each quadrat during summer 1994 included percent cover and density of exotics, percent canopy cover of trees and shrubs (using a spherical densiometer), percent cover of disturbance (disturbed bare ground, trampled grass, footprints, and social trails), and percent cover of bare ground and other vegetation. Additional data were collected and analyzed as reported by Allen (1996).

Distribution of exotic plant cover and density relative to distances from campground edges were displayed with side-by-side boxplots and scatterplots for campgrounds in which exotics were found. A Cox-Stuart test for trend (Daniel 1990) was used to determine the general trend in occurrence of exotics with increasing distance from the edge of Mammoth campground. Chi-square tests were used to determine whether significant associations existed between canopy cover and presence of exotics and between disturbance and presence of exotics ($\alpha = 0.05$ for all analyses).

RESULTS AND DISCUSSION

Species Distributions

Exotic plants were found in only 6 of 11 campgrounds (Mammoth, Slough Creek, Madison, Norris, Grant Village, and Bridge Bay). Six species were found at Mammoth (spotted knapweed, hound's-tongue, Canada thistle, dalmatian toadflax, yellow sweetclover, and common mullein). Canada thistle was found in all 6 campgrounds, while oxeye-daisy was found in just 1 quadrat at Norris campground. We observed no other exotics within the quadrats; however, we saw others in the vicinity.

Exotics and Distance from Campgrounds

Exotic plants at Mammoth campground were fairly numerous and occurred at all measured distances beyond the campground edge (Fig. 1). Few to no exotics were found within the quadrats placed immediately inside the campground edge (quadrats 0), due primarily to frequent and severe campground-associated disturbance. Exotic cover and density were higher immediately outside the campground edge (quadrats 1 and 2). Median exotic density and cover decreased from 2 m out to 4 m and 6 m, respectively, suggesting the campground may be a source of inoculation or introduction. This decrease in exotics with distance from disturbance is similar to results found by Dale and Weaver (1974), Benninger-Truax et al. (1992), and Tyser and Worley (1992). Beyond about 6 m, density and cover increased out to 9 m, and then became more variable. We found a general trend of higher density ($P = 0.001$) and cover ($P = 0.011$) at distances of 11–50 m (versus 0–10 m) from Mammoth campground edge. Canada thistle presence was

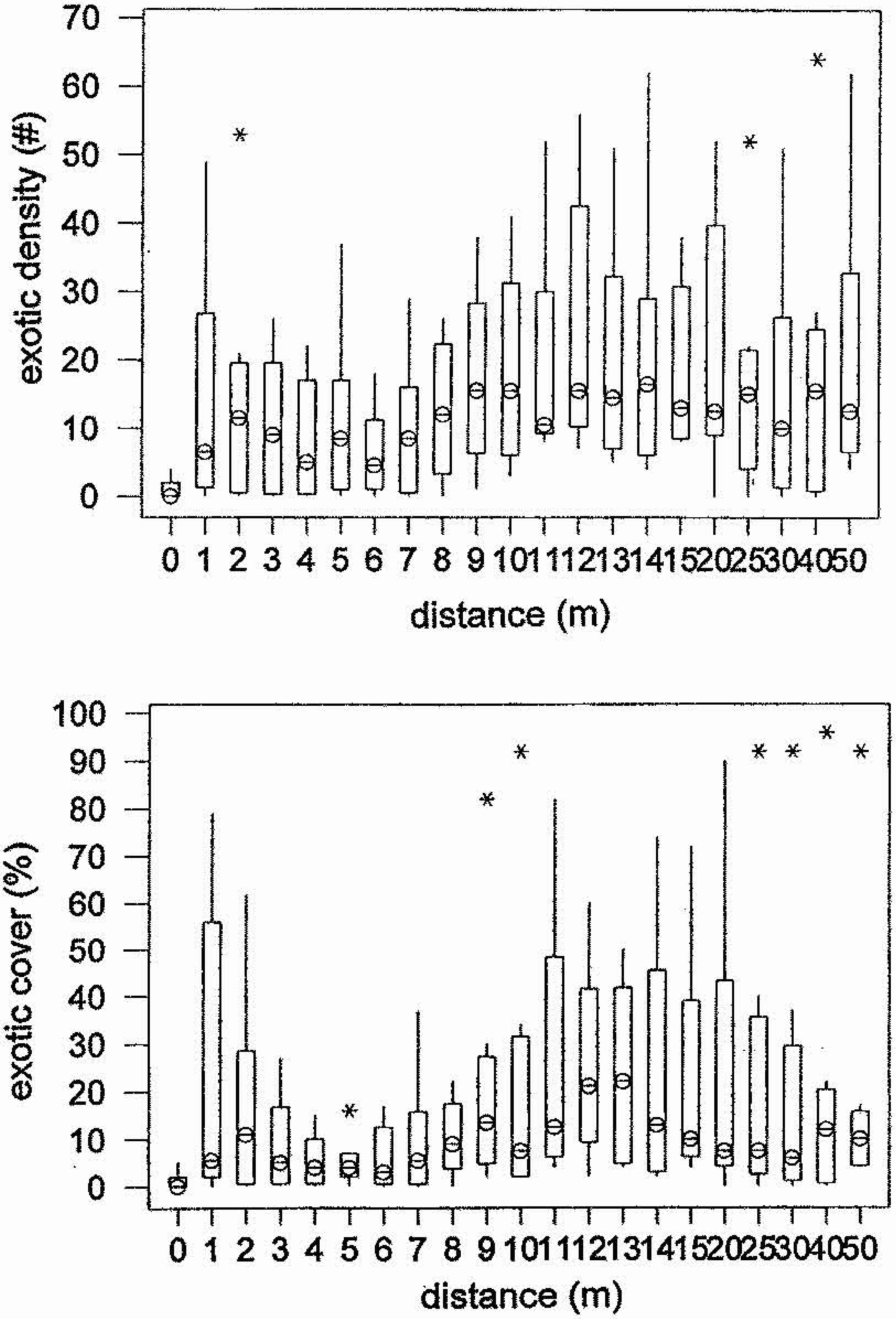

Fig. 1. Geography of exotic plants (density and cover) relative to distance from Mammoth campground edge.

highest between 11 m and 15 m, and between 30 m and 50 m, from campground edges, based on the cumulative relative frequency of Canada thistle relative to distance for all quadrats in which the plant was found. No decreasing trend in Canada thistle presence with distance was found.

Exotics and Canopy Cover

At Mammoth campground a significant association was found between canopy cover (at the 20% and 30% open/closed threshold divisions) and presence of hound's-tongue, spotted knapweed, and yellow sweetclover (Table 2). Hound's-tongue was significantly associated with closed canopies, suggesting the plant prefers or tolerates some degree of shade. It was more consistently found under higher canopy covers than any other exotic species (Fig. 2). This condition is similar to that reported by Lacey and Lacey (1986), where hound's-tongue was found in areas of

TABLE 2. Results of chi-square tests used to determine the association between canopy cover and exotic plant presence at Mammoth campground (*denotes significance at 0.05 level).

Exotic plant(s)	Canopy cover (%)	Chi-square	*P*-value
All	20	0.940	0.3323
	30	1.334	0.2481
	40	2.047	0.1525
Hound's-tongue	20	18.476	0.0000*
	30	5.483	0.0192*
	40	2.853	0.0912
Spotted knapweed	20	7.920	0.0049*
	30	3.859	0.0495*
	40	3.047	0.0809
Dalmatian toadflax	20	0.036	0.8495
	30	0.025	0.8744
	40	0.017	0.8963
Yellow sweetclover	20	19.313	0.0000*
	30	5.797	0.0161*
	40	3.053	0.0806
Mullein	20	2.098	0.1475
	30	2.208	0.1373
	40	1.743	0.1868
Canada thistle	20	0.355	0.5513
	30	0.173	0.6775
	40	0.137	0.7113

thick litter accumulation (as might be found under a forest with high canopy cover). Presence of spotted knapweed and yellow sweetclover was significantly associated with open canopy conditions (at the 20% and 30% open/closed threshold divisions). Spotted knapweed was always found under <20% canopy, and 75% of its occurrence fell below ≤5% canopy cover (Fig. 2). Previous studies have also found spotted knapweed to be more abundant under open canopies (Watson and Renney 1974, Losensky 1987, Milner 1995). Seventy-five percent of yellow sweetclover occurrences were beneath ≤10% canopy cover.

Dalmatian toadflax, found growing under a wide range of canopy covers, from 0% to 85%, was predominantly found under lower canopy cover values. While it is known to establish drier, open areas (Lajeunesse et al. 1993), results indicate its tolerance for moderate amounts of shade. Mullein was always found under a canopy cover of <30%, and 75% of its occurrences were under ≤5% canopy cover (Fig. 2). No significant association was found between canopy cover and mullein, nor between all exotics (when combined at Mammoth; Table 2), reflecting differences in canopy cover tolerance of individual species. In 84% of quadrats within which exotics were found, however, canopy cover was ≤30% (Fig. 2).

Eighty-seven percent of Canada thistle occurrences were under a canopy cover of ≤20%. Haderlie et al. (1989) found that warmth and long days favored Canada thistle growth. This condition is present in open canopy conditions during the Yellowstone National Park growing season. Although Canada thistle grows most often under open canopies, its occasional presence under more closed canopy covers (up to 95%) suggests it is somewhat tolerant of shade.

Exotics and Disturbance

Almost 40% of the quadrats at Mammoth contained no disturbance, and yet exotics were frequently encountered in these sites. In 75% of the disturbed quadrats at Mammoth, disturbance covered ≤20% of a quadrat. Presence of exotic plants at Mammoth was found to be significantly related to levels of disturbance of ≤20% ($P = 0.0002$). Exotics occurred most frequently at low disturbance covers partially because these are the conditions most commonly encountered at Mammoth. Higher disturbance covers (>60%) occurred infrequently and were usually found in the road edge disturbance of the 1st quadrat. Exotics were apparently less able to become established where disturbance levels were high.

Disturbance cover at Mammoth decreased from the campground edge out to a distance of 6 m. A general trend of decreasing exotic plant cover with increasing disturbance was found. In other studies it was often predetermined or assumed that disturbance decreased with distance from the road or trail, and that exotic presence decreased along this gradient (Weaver et al. 1989, Benninger-Truax et al. 1992). In this study the cover of disturbed ground was highest between 25 m and 40 m from Mammoth campground edge; however, highest exotic covers did not occur at comparable distances.

We found Canada thistle growing in all amounts of disturbance, although 20% of quadrats in which it was present had no evidence of disturbance. Canada thistle abundance increased as disturbance cover increased from 5% to 40%. No relationship was found between disturbance and Canada thistle when disturbance covers exceeded 60%. Where both Canada thistle and disturbance occurred, the

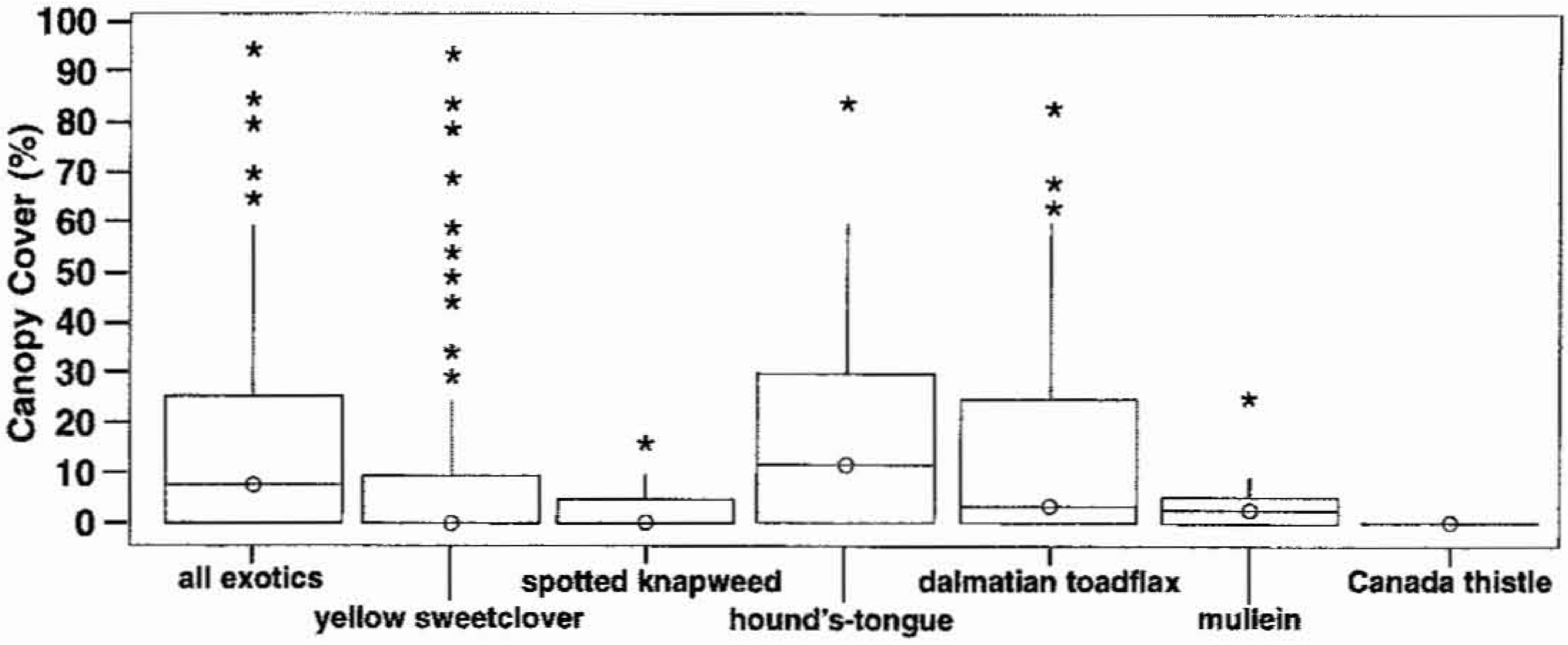

Fig. 2. Geography of canopy cover for all exotics—yellow sweetclover, spotted knapweed, hound's-tongue, dalmatian toadflax, mullein, and Canada thistle—where found at Mammoth campground.

plant was consistently rooted within the disturbance. The ability of Canada thistle to reproduce by lateral roots (Haderlie et al. 1989) may contribute to its presence in undisturbed and in both low and high levels of disturbed ground.

Patterns in exotic cover were explained, in part, by both canopy and disturbance. The highest exotic plant cover at Mammoth, in most transects, occurred where canopy and disturbance covers were both low. An exception to this occurred along 2 transects where a high percentage of hound's-tongue was found under canopies >25% (again indicating its tolerance of higher canopy covers).

Exotics and Other Vegetation

Exotic species were usually found growing with other plants, but overall the exotic plant cover at Mammoth decreased with an increase in individual covers of grasses, forbs, shrubs, and the combined cover of these vegetation forms. In contrast, 77% of Canada thistle occurrences were with at least 45% cover of other vegetation, and 33% of occurrences of Canada thistle were with ≥75% cover, suggesting Canada thistle can compete well for available resources. Overall, exotic cover was greatest where bare soil cover was ≤10%. When Canada thistle was present, bare soil always covered <40% of the quadrat. This result (more exotics where less bare soil is found) supports other results (reported above) for disturbance, as disturbance often produces bare soil. A slight decrease in exotic cover occurred with an increase in litter, and no relationship was found between exotic cover and that of moss/lichen, sedges, or trees.

Exotics and Habitat Type

Six exotic species were found in the big sagebrush/bluebunch wheatgrass habitat type, a lower-elevation, drier habitat type than others in Yellowstone (Table 1). Forcella and Harvey (1983) also found exotics to be common in low-elevation, dry habitats.

The abundance of exotics at Mammoth may be related to climate. Of all Yellowstone campgrounds, this site has the longest frost-free period (125 d) and the highest average temperatures (15.3°C) for the summer growing season (June–August; Natural Resources Conservation Service 1994). Spotted knapweed has been found to be more common at relatively low elevations (610–1829 m), and it requires 50–120 frost-free days (Chicoine et al. 1988, Milner 1995). Mammoth was the only campground that met these conditions.

Fewer exotic plants were found at higher elevations, perhaps due to shorter growing seasons, habitat types, and related higher canopy covers. Low temperatures have been shown to inhibit total germination and rate of germination in yellow sweetclover (McElgunn 1973). Oxeye-daisy is adapted to a more northern climate (Lindsay 1953) than that of Yellowstone National Park, perhaps explaining its presence at a higher elevation (2275 m) than most other exotics, in the subalpine fir/pinegrass habitat. Canada thistle was found in a wide range of habitats (big sagebrush/Idaho fescue, Douglas-fir/common snowberry, Engelmann spruce/sweetscented bedstraw, Engelmann spruce/horsetail, subalpine fir/grouse whortleberry, and subalpine fir/pinegrass habitats), a range of elevations (1820–2365 m), and on slopes ≤10%. No exotics were found in the subalpine fir/twinflower habitat.

Random and Control Quadrats

All 8 random quadrats sampled within Mammoth campground contained hound's-tongue, spotted knapweed, dalmatian toadflax, and yellow sweetclover. Canada thistle was found in 2 quadrats within Slough Creek campground. Control quadrats near Mammoth were the only ones that contained exotic plants. Five of these 8 contained dalmatian toadflax.

CONCLUSIONS

Results of this study provide new information about the (1) geography of exotics within Yellowstone National Park and (2) canopy conditions under which some exotics may grow. Exotic occurrence was limited adjacent to most of the park's campgrounds, but it was relatively high adjacent to Mammoth campground. Exotics decreased with distance from the campground edge, up to 6 m, and then increased. The large number of exotics found colonizing between 11 m and 50 m from Mammoth campground edge disturbance may be a result of several factors: availability of viable seed, habitat type, canopy cover, year-round use, and proximity to roads and trails. Distribution of exotics at Mammoth suggests that plants may spread outward from the campground area or from other nearby roads and trails. Canada thistle was the most prevalent species in all other campgrounds, covering a wide range of habitats.

Canopy cover and exotic occurrence were inversely related for most species; however, hound's-tongue, Canada thistle, and dalmatian toadflax were also found under more closed canopy conditions. Fewer exotics occurred as disturbance increased, and exotics were frequently encountered in areas of no disturbance. Because undisturbed or slightly disturbed ground is common under natural conditions, exotics can be expected to colonize these areas given a seed source and sufficient light and nutrients. Canada thistle was found, however, in all amounts of disturbance, suggesting that many areas are suitable for its establishment. Generally, exotics decreased with an increase in cover of other vegetation, perhaps due to increased competition for available nutrients, water, and light. Canada thistle appears to compete well, as indicated by its occurrence with high percentages of other vegetation.

Resource management activities in Yellowstone may have contributed to the geography of exotics as found in this study. Some spraying and pulling of exotics in campgrounds has occurred, but most control efforts have been concentrated along roadsides (J. Sweaney, North District Resource Management coordinator, Yellowstone National Park, personal communication 1996). Canopy cover within forested campgrounds of the park is being reduced as necessary to prevent "hazard trees" from falling. Although exotics were found adjacent to few campgrounds, and a relatively small number of species was found, there are indications that exotics are spreading. The results of this study may be applied to ecosystems similar to this national park and can serve as a baseline for evaluating human-induced changes elsewhere.

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